

TAXONOMIC STUDIES
IN THE ZINGIBERACEAE
WITH SPECIAL REFERENCE TO
VEGETATIVE CHARACTERS

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I. INTRODUCTION

The Zingiberaceae (sensu lato) is a large family with about one thousand and four hundred or more species distributed in about forty-seven genera. They are mostly distributed in the tropical and sub-tropical regions; only a few of the genera are represented in the colder regions of the World.

Despite the fact that the family has received much attention from different workers, its taxonomy is still far from being well understood. Three recent systems of classification only will be dealt with here. A synopsis of these classifications is summarised in Table 1.

The only monograph, on a world basis, which is still outstanding but rather unsatisfactory, is that produced by K. Schumann (1904) and published in Engler's Pflanzereich. This author recognised two sub-families, i.e. Zingiberoideae and Costoideae. He arranged the genera into four tribes, three in the Zingiberoideae, viz:- Globbeae, Hedychieae and Zingibereae (including the genus Zingiber), and the tribe Costeae in the Costoideae. Apart from these major sub-divisions there are many confusions at or below the generic level.

Holttum (1950) has revised the Zingiberaceae of the Malay Peninsula. Although this work was mainly concerned with one geographical region, the author adopted a new classification for the family. He recognised three tribes in the sub-family Zingiberoideae, viz:- Globbeae, Hedychieae and Alpinieae, the last two being different from Schumann's tribes. In this arrangement, Zingiber was transferred from the Zingibereae into Hedychieae. For this tribe the tribal name was retained as Hedychieae, because it was very different from Schumann's definition of Zingibereae. The remaining genera in

TABLE 1. THE DIFFERENT STYSTEMS OF CLASSIFICATION FOR THE ZINGIBERACEAE.
(A SYNOPSIS OF THE GENERA STUDIED)

K. SCHUMANN (1904)	HOLTUM (1950)	TOMLINSON (1956, 1969)	PROPOSED
FAMILY		ZINGIBERACEAE (sensu stricto)	ZINGIBERACEAE
SUB-FAMILY:- ZINGIBEROIDEAE	ZINGIBEROIDEAE		
TRIBE:- I. <u>GLOBBEAE</u>	<u>GLOBBEAE</u>	<u>GLOBBEAE</u>	I. <u>GLOBBEAE</u>
GLOBBA	GLOBBA		GLOBBA
MANTISIA	MANTISIA		MANTISIA
II. <u>HEDYCHIEAE</u>	<u>HEDYCHIEAE</u>	<u>HEDYCHIEAE</u>	II. <u>HEDYCHIEAE</u>
HEDYCHIUM	HEDYCHIUM		HEDYCHIUM
BRACHYCHILUM	BRACHYCHILUM		BRACHYCHILUM
CAMPTANDRA	CAMPTANDRA		CAMPTANDRA
KAEMPFERIA	KAEMPFERIA		→ CAULOKAEMPFERIA
			→ KAEMPFERIA
			→ CIENKOWSKYA
	SCAPHOCHLAMYS		SCAPHOCHLAMYS
HAPLOCHOREMA	HAPLOCHOREMA		HAPLOCHOREMA
GASTROCHILUS	→ BOESENBERGIA		BOESENBERGIA
HITCHENIA	HITCHENIA		HITCHENIA
CURCUMA	CURCUMA		CURCUMA
ROSCOEIA	ROSCOEIA		ROSCOEIA
CAUTLEYA	CAUTLEYA		CAUTLEYA
	ZINGIBER		III. <u>ZINGIBEREAE</u>
			→ ZINGIBER
III. <u>ZINGIBEREAE</u>	<u>ALPINIEAE</u>	<u>ALPINIEAE</u>	IV. <u>ALPINIEAE</u>
ZINGIBER			
HORNSTEDTIA	HORNSTEDTIA		HORNSTEDTIA
AFRAMOMUM	AFRAMOMUM		AFRAMOMUM
ANOMUM	ANOMUM		ANOMUM
PHAEOMERIA	PHAEOMERIA		PHAEOMERIA
ELETTARIA	ELETTARIA		ELETTARIA
CYPHOSTIGMA	CYPHOSTIGMA		CYPHOSTIGMA
GEOSTACHYS	GEOSTACHYS		GEOSTACHYS
GEOCHARIS	GEOCHARIS		GEOCHARIS
BURBIDGEA	BURBIDGEA		BURBIDGEA
RENEALMIA	RENEALMIA		RENEALMIA
ALPINIA	(ALPINIA		(ALPINIA
	(CATIMBIUM		(CATIMBIUM
	(CENOLOPHON		(CENOLOPHON
	(LANGUAS		(LANGUAS
ACHASMA	ACHASMA		ACHASMA
PLAGIOSTACHYS	PLAGIOSTACHYS		PLAGIOSTACHYS
ADELMERIA	ADELMERIA		ADELMERIA
SUB-FAMILY:- COSTOIDEAE	COSTOIDEAE	FAMILY:-COSTACEAE	FAMILY:-COSTACEAE
TRIBE:- IV. <u>COSTEAE</u>	<u>COSTEAE</u>		
COSTUS	COSTUS		COSTUS
TAPEINOCILUS	TAPEINOCILUS		TAPEINOCILUS

Schumann's Zingibereae (i.e. without Zingiber) were given the tribal name Alpinieae. As will be discussed later, this treatment was contrary to the Code of Botanical Nomenclature (Art. 19). A new treatment for the genus Zingiber is proposed in this study.

Another important change in the classification of the family in recent years, came from the work of Tomlinson (1956, 1969) on the Systematic anatomy. This author, following similar suggestion by Nakai (1941), elevated the two sub-families Zingiberoideae and Costoideae to familial rank as Zingiberaceae and Costaceae respectively. The anatomical observations made by me support the separation into two families.

The past classifications of the family have been based entirely on floral features, and only in a few cases do the vegetative characters feature in the keys to the genera. The identification of herbarium materials without good floral parts is often impossible. As is well known to many collectors and workers in this family, the floral biology of the plants is such that the flowers do not preserve well and long, without special care, and those mounted on herbarium sheets often lose their important details. The collection of floral parts needs adequate care and measures like spirit preservation to ensure the availability of good specimens for study.

The main problems in the present investigation are the identification, and generic delimitation and relationships of the members of this family.

The anatomy of the family was studied by Solereder and Meyer (1930) and recently by Tomlinson (1956, 1969). The number of species investigated by the last worker was forty-one, as compared with more than one thousand two hundred and fifty species in the Zingiberaceae (sensu stricto).

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GLOBBA	GLOBBA		GLOBBA
MANTISIA	MANTISIA		MANTISIA
II. <u>HEDYCHIEAE</u>	<u>HEDYCHIEAE</u>	<u>HEDYCHIEAE</u>	II. <u>HEDYCHIEAE</u>
HEDYCHIUM	HEDYCHIUM		HEDYCHIUM
BRACHYCHILUM	BRACHYCHILUM		BRACHYCHILUM
CAMPTANDRA	CAMPTANDRA		CAMPTANDRA
KAEMPFERIA	KAEMPFERIA		→ CAULOKAEMPFERIA
			→ KAEMPFERIA
			→ CIENKOWSKYA
HAPLOCHOREMA	SCAPHOCHLAMYS		SCAPHOCHLAMYS
GASTROCHILUS	HAPLOCHOREMA		HAPLOCHOREMA
HITCHENIA	→ BOESENBERGIA		BOESENBERGIA
CURCUMA	HITCHENIA		HITCHENIA
ROSCOEIA	CURCUMA		CURCUMA
CAUTLEYA	ROSCOEIA		ROSCOEIA
	CAUTLEYA		CAUTLEYA
	ZINGIBER		III. <u>ZINGIBEREAE</u>
			→ ZINGIBER
III. <u>ZINGIBEREAE</u>	<u>ALPINIEAE</u>	<u>ALPINIEAE</u>	IV. <u>ALPINIEAE</u>
ZINGIBER			
HORNSTEDTIA	HORNSTEDTIA		HORNSTEDTIA
AFRAMOMUM	AFRAMOMUM		AFRAMOMUM
AMOMUM	AMOMUM		AMOMUM
PHAEOMERIA	PHAEOMERIA		PHAEOMERIA
ELETTARIA	ELETTARIA		ELETTARIA
CYPHOSTIGMA	CYPHOSTIGMA		CYPHOSTIGMA
GEOSTACHYS	GEOSTACHYS		GEOSTACHYS
GEOCHARIS	GEOCHARIS		GEOCHARIS
BURBIDGEA	BURBIDGEA		BURBIDGEA
RENEALMIA	RENEALMIA		RENEALMIA
ALPINIA	(ALPINIA		(ALPINIA
	(CATIMBIUM		(CATIMBIUM
	(CENOLOPHON		(CENOLOPHON
	(LANGUAS		(LANGUAS
ACHASMA	ACHASMA		ACHASMA
PLAGIOSTACHYS	PLAGIOSTACHYS		PLAGIOSTACHYS
ADELMERIA	ADELMERIA		ADELMERIA
SUB-FAMILY:- COSTOIDEAE	COSTOIDEAE	FAMILY:-COSTACEAE	FAMILY:-COSTACEAE
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The main aim of this study is to review the vegetative anatomy by

examining many more specimens than has previously been done, and to find anatomical characters that may be useful for reinforcing the already recognised floral characters of the genera. Some characters that may be useful for this purpose have been observed in this investigation. Furthermore, some generic groupings have been produced on the basis of their anatomical similarities, but such groupings do not necessarily represent a new classification.

The family Zingiberaceae (*sensu stricto*) is probably well suited for this type of investigation. This is because, although there are still many taxonomic problems which can only be tackled on a floral basis, most of the genera are well defined on floral features. Such a family affords an interesting platform for estimating the value of anatomical studies in the taxonomy of a monocotyledonous family highly specialised and varied in floral structure.

The role of anatomy in taxonomy is a very important one, and has been the subject of many symposia and discussions. Many workers, such as Metcalfe and Chalk (1950), Metcalfe 1960, 1963, 1968, Tomlinson 1956, 1961, 1969, and Outler 1969, have contributed in no small way to our knowledge of the systematic anatomy of the Angiosperms. Metcalfe and Chalk (1950) in their two volumes on the Anatomy of the dicotyledons, described anatomical features as the tool with which to explore possible evolutionary progression. Also, Davis and Heywood (1963) showed that anatomical characters play an increasingly important role in the formulation of natural or phenetic groups.

Anatomical data can be employed in Zingiberaceae taxonomy as follows:-

- (1) For the preliminary identification of herbarium materials, particularly

sterile or fragmentary materials, i.e. without floral organs on which the classification of the group was previously based.

(ii) To effect an improvement to the existing systems of classification through readjustments and modifications where these are justified on anatomical grounds. Anatomical features may be useful for detecting the true affinities between the various taxa in a family where such may be obscured by convergence in floral features. On the other hand, anatomical features may lead to different conclusions by suggesting new treatments to be accorded some genera or species when such treatments might not be obvious on a floral basis.

The interesting anatomical characters observed in this investigation should contribute to the improvements of the taxonomy of the Zingiberaceae.

II. MATERIALS AND METHODS

The vegetative materials for about 305 species were examined for this study. Most of the materials were taken from the herbarium specimens, except where the fresh materials for about 45 species were collected from those cultivated in the glass houses of the Royal Botanic Gardens, Edinburgh. The list of the species examined, the collector's name and number, and the locality of the specimens, is included in the appendix.

Anatomical investigations were made on species which have been identified, at least, to the genus. Herbarium materials were revived by boiling for 10 - 20 minutes in water to which a few drops of the wetting agent, 'teepol', was added. Both fresh and revived materials were fixed and kept in formol-acetic acid-alcohol solution (F.A.A.).

For the purposes of comparative studies the materials were taken from the standard median levels on the sheath, stem, petiole and lamina. Old and moderately sized roots were preferred to young ones. The nature of the rhizome makes it difficult to lay down a standard level. However, all transverse sections were taken from the median portion of the rhizome elements available. Some of the hard and woody rhizome elements were softened overnight in 4% hydrofluoric acid before sectioning.

Epidermal peels were made from both surfaces of the lamina. The specimen was held down, with a pair of blunt forceps, on to a glazed tile. The tissues on top of the epidermis were scraped off with a sharp scalpel or razor blade held at an angle. Loose cells were brushed away from this preparation by using water and soft camel hair brush. The epidermal peels from the sheath, petiole and midrib of the lamina were removed by sharp razor blades. All the epidermal peels were cleared in 25% domestic

parozone (sodium hypochlorite) for at least 5-10 minutes. The specimens were then washed several times in water.

Most transverse sections were made by freehand method. Some specimens were cut on the sledge microtome and their thickness varies between 15-60 μ . Some of the sections were stained or mounted in glycerine solution without clearing, while most others were cleared, and washed before staining them.

Some permanent preparations were made in the following common staining procedures; (a) Safranin/fast green, (b) Safranin/Delafield's haematoxylin, (c) Phloroglucinol and conc. HCl. Most of the specimens were stained in 1% Safranin in 50% alcohol and mounted temporarily in diluted glycerine solution. Such preparations keep well for the period of the investigation.

For the different chemical constituents of the cell walls and contents of the cells, the following tests were performed:

- (i) For suberized cell walls, the specimens were stained in Sudan IV solution.
- (ii) The oil cells were investigated by using Iugol's iodine method. The specimens were placed on a slide and flooded with aqueous Iugol's iodine (I_2KI). This was covered with a cover slip. Few drops of 70% H_2SO_4 were added to one side of the cover slip and drawn over the specimen by using a filter paper on the opposite side. The walls of the oil cells stained yellow while those of the other cellulose walls stained blue. Other suberized and cutinized walls also stained yellow.
- (iii) Some of the specimens were investigated for tannin deposits in the cells. The transverse sections of the fresh and herbarium materials were placed in aqueous solution of Ferric chloride, to

which a little sodium carbonate was added. The cells containing tannins gradually turned blue-green in colour, indicating the presence of tanniniferous substances.

- (iv) For Calcium oxalate crystals, the epidermal peels or transverse sections of the specimens were placed on the slide with a few drops of freshly made saturated solution of Cupric acetate. The crystals were observed under the microscope as they dissolve in the solution. Confirmatory tests were performed on few specimens. Few drops of Ferric sulphate solution (5 grams Ferric sulphate dissolved in 80 cc. water + 20 cc. acetic acid), were added to the test specimens. Yellow crystals of Ferrous sulphate were produced which confirms the presence of Calcium oxalate.
- (v) For the silica bodies, the transverse sections of the lamina were placed on a slide and covered by few phenol crystals. The slide was heated and red-pinkish colour was produced around the silica bodies, which shows the presence of Silicon.

For the study of the vascular elements, small pieces of the root, rhizome, true stem, sheath and lamina were macerated in Chromic/nitric acid mixture at 60°C for about 24-48 hours depending on the toughness of the materials. Some materials were macerated more rapidly by heating them in 10% Potassium hydroxide solution for about half to two hours. The specimens were washed many times and allowed to stand in "Eau de Javelle", a clearing agent for about half to one hour. The specimens were then washed several times with water, stained in 1% Safranin in 50% alcohol and mounted temporarily in diluted glycerine solution.

Very few specimens were embedded in paraffin wax for serial sectioning.

The common method of embedding was employed. The transverse and longitudinal sections made from the embedded materials were stained either in Safranin/Delafield's haematoxylin or Safranin/fast green stain combination.

Illustrations were made from some of the slides by drawing through an optical camera lucida. Some photographs of the important features were also prepared.

Suggestions for future collections in the family.

It was observed that by far the greatest number of the herbarium specimens for the family were incomplete and many others were represented only by fragmentary parts of some organs. It cannot be over-emphasized that, for both floral and anatomical investigations, the complete mature plants are very essential. The large size of the plants in some genera may constitute some major problems of housing such specimens on the herbarium sheets. But, the materials could be collected from the major standard levels on the root, rhizome, pseudostem, lamina and inflorescence axis; and such materials should be accompanied by good field notes of those features which might be unobtainable or those that may be lost on the dried plants. Where the subterranean organs are fleshy and bulky, these materials may be treated in the same way as the carpological collections.

III. CHARACTERS, THEIR DISTRIBUTION AND VARIATION

A. EXTERNAL MORPHOLOGY

THE RHIZOME AND ROOT

The characteristics of the rhizome have been the topics of special study for a long time, particularly by pharmacognosists who were interested in the economic and medicinal properties of these organs. The rhizome may be subterranean, as in Globba, Zingiber, and Alpinia; it may be just above the ground as in Hedychium (except in the epiphytic species); or it may be raised above the ground by stilt roots as in some species of Scaphochlanys, Anomum and Hornstedtia. The depth to which the rhizome grows may be characteristic of certain genera such as Achasma and Roscoea whose rhizomes are deeply buried.

The rhizome is sympodially branched. The new rhizome elements develop laterally from the buds in the axils of the scale leaves which are very close to the base (fig. 1.A,B) of the old vegetative shoot. The nature of the development of the rhizome elements were studied in some detail by Halle (1967) on Aframomum polyanthum (K. Schum) K. Schum and Costus diklagei K. Schum, species from Gabon and Cameroons respectively. Some observations were made on the development of the rhizome elements and inflorescence axes of some species in the family.

In those genera with short rhizomes, e.g. Globba, Kaempferia, Curcuma and Boesenbergia, the developing bud becomes swollen very close to the older rhizome segment. This swollen part forms the rhizome base of the new plant while the apical part rapidly turned upwards and produces, at first blade-less sheaths but gradually, sheaths with expanded lamina were formed. In those genera with longer and well spreading rhizomes, as in

ATTORNEYS AT LAW

60 TWENTY NINE

1998, 1999, 2000, 2001, 2002, 2003, 2004, 2005, 2006, 2007, 2008, 2009, 2010, 2011, 2012, 2013, 2014, 2015, 2016, 2017, 2018, 2019, 2020, 2021, 2022, 2023, 2024, 2025, 2026, 2027, 2028, 2029, 2030, 2031, 2032, 2033, 2034, 2035, 2036, 2037, 2038, 2039, 2040, 2041, 2042, 2043, 2044, 2045, 2046, 2047, 2048, 2049, 2050, 2051, 2052, 2053, 2054, 2055, 2056, 2057, 2058, 2059, 2060, 2061, 2062, 2063, 2064, 2065, 2066, 2067, 2068, 2069, 2070, 2071, 2072, 2073, 2074, 2075, 2076, 2077, 2078, 2079, 2080, 2081, 2082, 2083, 2084, 2085, 2086, 2087, 2088, 2089, 2090, 2091, 2092, 2093, 2094, 2095, 2096, 2097, 2098, 2099, 2100, 2101, 2102, 2103, 2104, 2105, 2106, 2107, 2108, 2109, 2110, 2111, 2112, 2113, 2114, 2115, 2116, 2117, 2118, 2119, 2120, 2121, 2122, 2123, 2124, 2125, 2126, 2127, 2128, 2129, 2130, 2131, 2132, 2133, 2134, 2135, 2136, 2137, 2138, 2139, 2140, 2141, 2142, 2143, 2144, 2145, 2146, 2147, 2148, 2149, 2150, 2151, 2152, 2153, 2154, 2155, 2156, 2157, 2158, 2159, 2160, 2161, 2162, 2163, 2164, 2165, 2166, 2167, 2168, 2169, 2170, 2171, 2172, 2173, 2174, 2175, 2176, 2177, 2178, 2179, 2180, 2181, 2182, 2183, 2184, 2185, 2186, 2187, 2188, 2189, 2190, 2191, 2192, 2193, 2194, 2195, 2196, 2197, 2198, 2199, 2200, 2201, 2202, 2203, 2204, 2205, 2206, 2207, 2208, 2209, 2210, 2211, 2212, 2213, 2214, 2215, 2216, 2217, 2218, 2219, 2220, 2221, 2222, 2223, 2224, 2225, 2226, 2227, 2228, 2229, 2230, 2231, 2232, 2233, 2234, 2235, 2236, 2237, 2238, 2239, 2240, 2241, 2242, 2243, 2244, 2245, 2246, 2247, 2248, 2249, 2250, 2251, 2252, 2253, 2254, 2255, 2256, 2257, 2258, 2259, 2260, 2261, 2262, 2263, 2264, 2265, 2266, 2267, 2268, 2269, 2270, 2271, 2272, 2273, 2274, 2275, 2276, 2277, 2278, 2279, 2280, 2281, 2282, 2283, 2284, 2285, 2286, 2287, 2288, 2289, 2290, 2291, 2292, 2293, 2294, 2295, 2296, 2297, 2298, 2299, 2300, 2301, 2302, 2303, 2304, 2305, 2306, 2307, 2308, 2309, 2310, 2311, 2312, 2313, 2314, 2315, 2316, 2317, 2318, 2319, 2320, 2321, 2322, 2323, 2324, 2325, 2326, 2327, 2328, 2329, 2330, 2331, 2332, 2333, 2334, 2335, 2336, 2337, 2338, 2339, 2340, 2341, 2342, 2343, 2344, 2345, 2346, 2347, 2348, 2349, 2350, 2351, 2352, 2353, 2354, 2355, 2356, 2357, 2358, 2359, 2360, 2361, 2362, 2363, 2364, 2365, 2366, 2367, 2368, 2369, 2370, 2371, 2372, 2373, 2374, 2375, 2376, 2377, 2378, 2379, 2380, 2381, 2382, 2383, 2384, 2385, 2386, 2387, 2388, 2389, 2390, 2391, 2392, 2393, 2394, 2395, 2396, 2397, 2398, 2399, 2400, 2401, 2402, 2403, 2404, 2405, 2406, 2407, 2408, 2409, 2410, 2411, 2412, 2413, 2414, 2415, 2416, 2417, 2418, 2419, 2420, 2421, 2422, 2423, 2424, 2425, 2426, 2427, 2428, 2429, 2430, 2431, 2432, 2433, 2434, 2435, 2436, 2437, 2438, 2439, 2440, 2441, 2442, 2443, 2444, 2445, 2446, 2447, 2448, 2449, 2450, 2451, 2452, 2453, 2454, 2455, 2456, 2457, 2458, 2459, 2460, 2461, 2462, 2463, 2464, 2465, 2466, 2467, 2468, 2469, 2470, 2471, 2472, 2473, 2474, 2475, 2476, 2477, 2478, 2479, 2480, 2481, 2482, 2483, 2484, 2485, 2486, 2487, 2488, 2489, 2490, 2491, 2492, 2493, 2494, 2495, 2496, 2497, 2498, 2499, 2500, 2501, 2502, 2503, 2504, 2505, 2506, 2507, 2508, 2509, 2510, 2511, 2512, 2513, 2514, 2515, 2516, 2517, 2518, 2519, 2520, 2521, 2522, 2523, 2524, 2525, 2526, 2527, 2528, 2529, 2530, 2531, 2532, 2533, 2534, 2535, 2536, 2537, 2538, 2539, 2540, 2541, 2542, 2543, 2544, 2545, 2546, 2547, 2548, 2549, 2550, 2551, 2552, 2553, 2554, 2555, 2556, 2557, 2558, 2559, 2560, 2561, 2562, 2563, 2564, 2565, 2566, 2567, 2568, 2569, 2570, 2571, 2572, 2573, 2574, 2575, 2576, 2577, 2578, 2579, 2580, 2581, 2582, 2583, 2584, 2585, 2586, 2587, 2588, 2589, 2590, 2591, 2592, 2593, 2594, 2595, 2596, 2597, 2598, 2599, 2600, 2601, 2602, 2603, 2604, 2605, 2606, 2607, 2608, 2609, 2610, 2611, 2612, 2613, 2614, 2615, 2616, 2617, 2618, 2619, 2620, 2621, 2622, 2623, 2624, 2625, 2626, 2627, 2628, 2629, 2630, 2631, 2632, 2633, 2634, 2635, 2636, 2637, 2638, 2639, 2640, 2641, 2642, 2643, 2644, 2645, 2646, 2647, 2648, 2649, 2650, 2651, 2652, 2653, 2654, 2655, 2656, 2657, 2658, 2659, 2660, 2661, 2662, 2663, 2664, 2665, 2666, 2667, 2668, 2669, 2670, 2671, 2672, 2673, 2674, 2675, 2676, 2677, 2678, 2679, 26

DI FUE

FIG. 1. PLANT HABIT.

- A. Aframomum sp. (B 4634) - Rhizome elements.
- B. Diagrammatic representation of the branching of the rhizome elements and inflorescence axes.
- C. Boesenbergia sp. (B & M 1564) - Prostrate rhizome with alternate branching; swellings on sheath surface.

infl. = inflorescence axis.

x = vegetative shoot.

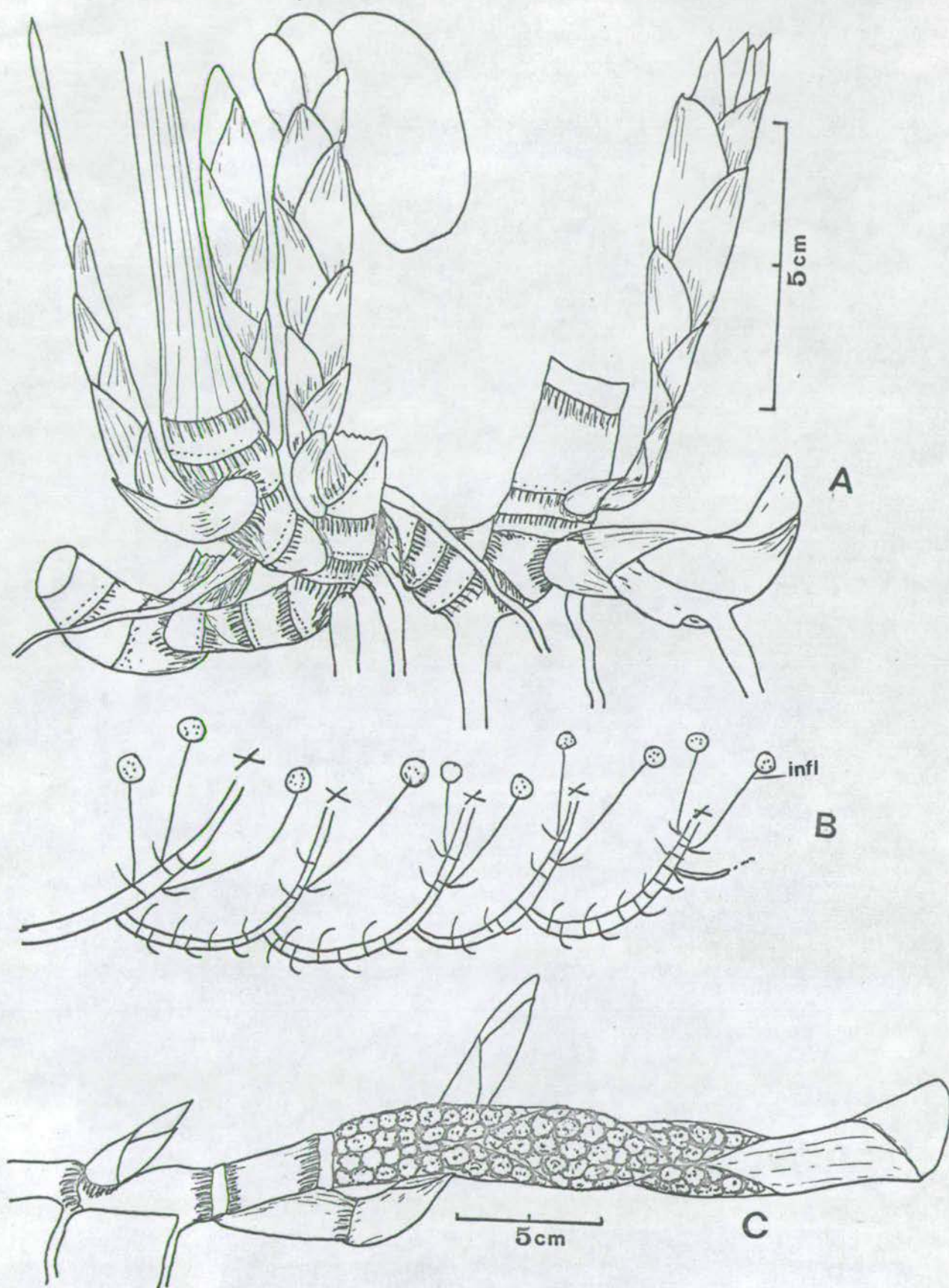


Fig-1

Cautleya, Roscoea, Alpinia and Aframomum, the developing element first produced a stoloniferous structure, of about 3-12 internodes long, which grows downwards at first but later becomes plagiotropic (fig. 1.A;2.F). The portion behind the apex becomes swollen very rapidly and forms the rhizome base of the new shoot at some distance from the parent plant. The apex develops in the same way as in the rhizome described. Adventitious roots and renewal buds for the following season were produced from the rhizome. In the genera mentioned above, more than one rhizome element may be produced and are disposed round the parent element in an alternate or zig-zag pattern, although the main growing point becomes determinate at the death of the current year's vegetative shoot.

The inflorescence axis may also develop in two ways; (i) where the flowers are born terminally on the vegetative shoots, as in Globbeae, Hedychieae, a number of species in Zingiber, Alpinia and Amomum, the vegetative shoot develops as described above. (ii) where the inflorescence axes are produced as separate organs from the vegetative shoot, they develop laterally from the buds in the axils of the scale leaves in the same way as the vegetative shoots are produced. But the buds which give rise to the inflorescence axes are, however, developed at some distance up the base of the current year's growth (fig. 1.A,B). Where there are more than one such separate inflorescence axes are produced alternately.

The rhizomes are the organs of perennation and storage. Swollen, fleshy, or slightly fleshy rhizomes are found in many genera of the tribe Hedychieae (fig. 2.A), except Scaphochlamys (Plate 1.A) Burbridgea and some species of Boesenbergia. Also, fleshy rhizomes are common among the species of Zingiber. Woody rhizomes are probably characteristic of all the genera

of the tribe Alpinieae except Phaeomeria with fleshy rhizomes which resemble those of Zingiber and Hedychium.

There are some differences among the genera with fleshy rhizomes in the level of development of these organs and root tubers. In Hedychium (fig. 2.A) Zingiber and Curcuma, the rhizome complex is massive and occupies a wider area around the growing shoots. Whereas, the rhizome is still fleshy in Globba and Kaempferia (fig. 2.C,D) it is much reduced in size. The rhizome is greatly contracted to a basal stock in Roscoeae (Plate 1.D; fig. 2.C) Kaempferia (fig. 2.D), Caulokaempferia, Camptandra, Boesenbergia, Cienkowskya (African Kaempferia) and Cautleya (fig. 2.F).

Root tubers are not well developed in Hedychium and rarely produced in Zingiber (except in Z. capitatum). Whereas, root tubers are well developed in Roscoeae (Plate 1.D; fig. 2.C), Caulokaempferia, Cautleya, Kaempferia, Cienkowskya, Curcuma (fig. 2.B) and Globba (fig. 2.E).

As could be seen from the above observation, there appears to be a gradual transference of the storage function from the rhizome, as seen in Hedychium and Zingiber, to the roots as in Globba, Roscoeae, Caulokaempferia, etc. In these latter genera, the rhizome has become greatly reduced in size to what could be called a 'renewal stock' to which the root tubers are attached.

The root tubers vary in shape and size in the different species. Long pendulous tubers are common in Curcuma (fig. 2.B) whereas sessile tubers are characteristic of Globba (fig. 2.E), Roscoeae (fig. 2.C) and Cautleya (fig. 2.F). The shape may be ovoid (fig. 2.C), cylindrical (fig. 2.F) or ellipsoidal (fig. 2.B). These differences in shape are probably useful for specific separation within a genus.

FIG. 2. RHIZOME AND ROOT TUBERS.

Explanation in the text.

- A. Hedychium gardnerianum.
- B. Curcuma longa.
- C. Roscoea cautleoides.
- D. Kaempferia pulchra.
- E. Globba atrosanguinea.
- F. Cautleya robusta.

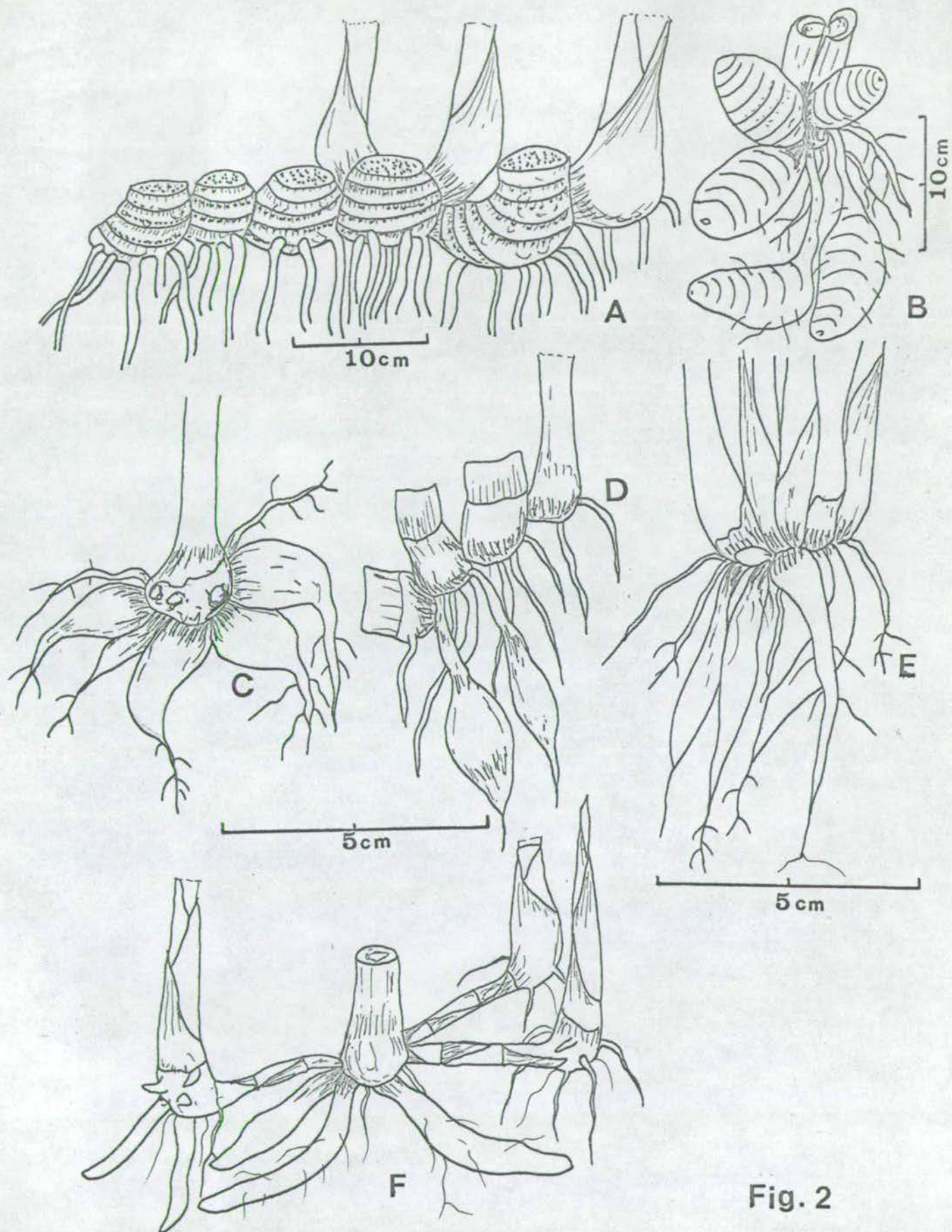


Fig. 2

PSEUDOSTEM AND TRUE STEM

Within the Zingiberaceae, there are two pseudostem organisations to be found. These are; (1) the compact, tall pseudostem, and (2) the loose, dwarf pseudostem.

(1) The compact and tall pseudostem (Plate 2.A) which is composed of closely clasping and concentric sheaths; the overall length of the sheath and lamina is never greater than that of the frond; the petiole is usually short; the leaf blades are held more or less horizontally; the true stem is developed to a variable height within the clasping sheaths.

This type of pseudostem is typical of the family and it is found in the tribes Globbeae, Zingibereae (i.e. Zingiber), Alpinieae, and some genera in the Hedychieae.

(2) Loose and dwarf pseudostem (Plate 1.A-C) which is composed of sheaths that are more or less loosely clasping, or sheaths that are not closely compacted throughout their length; they are, instead, separate from each other and erect from or near the base. The real pseudostem is short, never more than one metre in height; the overall length of the sheath and blade is greater than that of the pseudostem and the latter is usually compressed. The petiole is usually long, (Plate 1.A,B) but short in some cases, (Plate 1.C), the blades are few, between one and eight per plant, and are held in a more or less erect position. The true stem is poorly developed or absent, the internode not being extended except when the inflorescence axis is produced.

This type of pseudostem is characteristic of Scaphochlamys, Curcuma, Hitchenia, Stahlianthus, Kaempferia, Boesenbergia, to a more or less extent in Camptandra, and occurs in Alpinia pumila, Cyphostigma and Elettariopsis.

PLATE 1. PSEUDOSTEM ORGANIZATION.

Explanation in the text.

- A. Scaphochlamys atroviridis.
- B. S. perakensis.
- C. Kaempferia elegans.
- D. Roscoe^ea chamaelon.

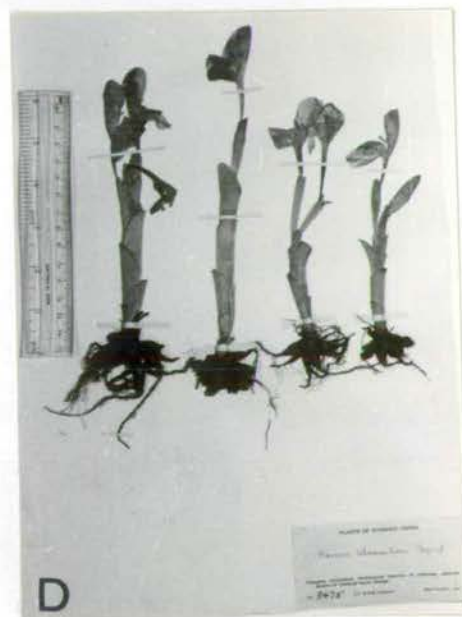


Plate 1

The first seven genera belong to the tribe Hedychieae and the last three to the Alpinieae. The diversity in the pseudostem organisation has been known and described for some time now (Holtum 1950), but up till the present moment, it has not been used for suggesting a sub-division for the dwarf genera within the Hedychieae. The seven genera referred to here have many features in common and they form a natural assemblage of closely related entities.

The surface of the sheath in the Globbeae, Alpinieae and a few genera in the Hedychieae, is usually striated. The longitudinal veins are conspicuously ribbed on the surface. In the Hedychieae, e.g. Curatma, Kaempferia, the longitudinal veins are less ribbed and the surface is more or less smooth. Sometimes the transverse veinlets are represented as green bands beneath the epidermis as in Kaempferia. On the sheath of most species of Hornstedtia, and a few species of Amomum, Alpinia, Riedelia and Cenolophon, the transverse veinlets are raised above the surface (fig. 13.g). These veinlets together with the velvety hairs, which have been discussed on page 76, give a characteristic pattern to the surface of the sheath, ligule and floral bracts of most species in Hornstedtia and may be diagnostic for this genus.

LIGULE.

The ligule is developed at the junction between the distal end of the sheath and the petiole. In some cases there is a gradual transition from the sheath to the ligule and the margins of the sheath are continuous with those of the ligule. There are about five types of ligule depending on the degree of development and shape. The ligule may be developed as;

- (i) narrow band between the sheath and petiole or lamina,
- (ii) sheath auricles,

FIG. 3. TYPES OF LIGULE.

Explanation in the text.

- A. Roscoeia auriculata.
 - B. & C. Curcuma longa.
 - D. Boesenbergia apiculatum.
 - E. & F. Alpinia mutica.
 - G. Hedychium coronarium.
 - H. & I. Renealmia racemosa.
 - J. & K. Zingiber officinale.
 - L. & M. Camptandra parvula.
- li = ligule. pul = 'pulvinus'

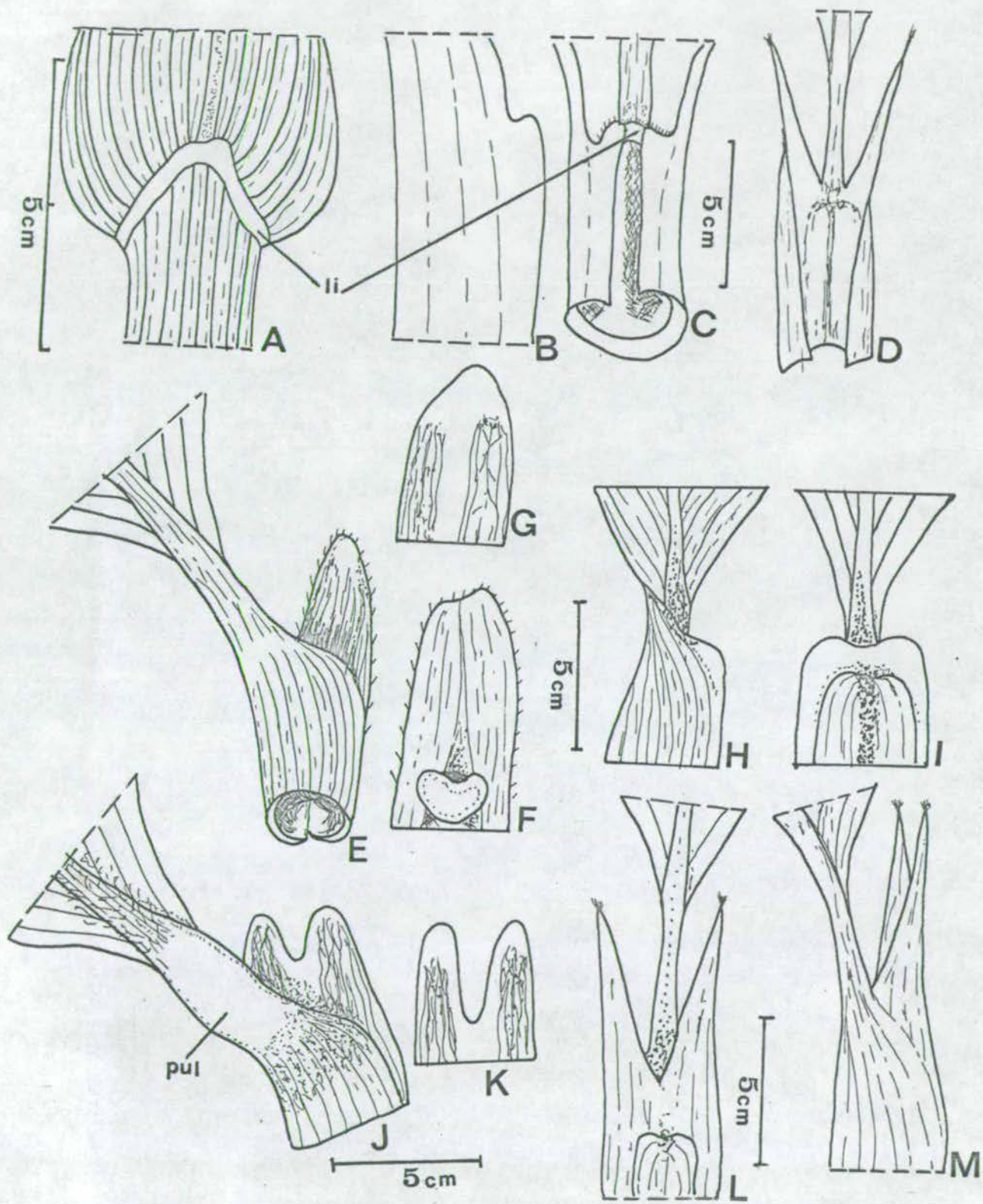


Fig.3

OR the shape may be:

- (iii) entire
- (iv) broad/emarginate and
- (v) bilobed.

(i) The ligule is developed as a narrow band between the sheath and the lamina in most species of Roscoea (fig. 3.A), Kaempferia angustifolia, K. gilbertii, Mantisia wardii, Curcuma and Scaphochlamys. In these genera the ligule is usually thinly membranous, inconspicuous and the length is never more than 10 mm.

(ii) The sheath margins may narrow gradually into two auricles at their distal ends. The connecting bridge may or may not be developed between these auricles. Where this is not developed, the ligules are truly auriculate as in Boesenbergia apiculatum (fig. 3.D) and B. striatum. Where the connecting bridge is developed then this type may be difficult to distinguish from the bilobed ligules as in some species of Curcuma (fig. 3.B,C).

(iii) The ligule may be entire (fig. 3.E-G) as in Hedychium, Brachychilum, a few species in Zingiber and most genera of the Alpinieae, e.g. Amomum and Aframomum. The apex of the ligule may be slightly undulate as in Hedychium or it may be split as in Alpinia mutica (fig. 3.F).

(iv) Broad or emarginate ligules (fig. 3.H,I) are characteristic of most species of Globba and Renealmia.

(v) The ligule may be bilobed (fig. 3.J,K) with deep or shallow lobes. The lobes may be round or obtuse as in most species of Zingiber (fig. 3.J,K), Burbridgea, Cautleya and Adelmeria bifida; or triangular or acute as in Boesenbergia (fig. 3.L,M), Scaphochlamys and Plagiostachys. There is great variation in the length of the ligule. In Roscoea, it varies between 0.5 - 3 mm. and in Hedychium it may reach up to 30-75 mm. as in H. cylindricum.

The ligule probably enables the distal parts of the sheath to be firmly clasped together and also supports the lamina which may be large and heavy in some genera. The ligule, because of its slightly concave shape, produces a suction pressure which ensures a firm adhesion for the distal parts of the sheath on the pseudostem. That this is true may be observed in the difficulty experienced by pulling the lamina away from a living plant. In the dwarf genera of the Hedychieae, e.g. Curcuma, Scaphochlamys, the ligule does not clasp the pseudostem because the sheaths, as discussed earlier, are separate from one another and compact pseudostem is almost lacking. Therefore, the strengthening function discussed above is not applicable to the ligule of these genera.

PETIOLE.

In most genera the sheath is usually separated from the lamina by a long or short petiole and sometimes the lamina may be sessile. But in some cases, the sheath and lamina are confluent and the petiole is conspicuously absent as in Roscoea (fig. 3.A), Kaempferia angustifolia, K. gilbertii and Mantisia wardii. In these genera, the base of the lamina is usually marked by the inconspicuous and membranous ligule. The base of the lamina may wrap round the stem and in this way the ligule is hidden under it as in Roscoea auriculata and Mantisia wardii. The characteristic absence of the petiole is probably a valuable generic character for Roscoea.

The length of the petiole varies in the different genera and species. In Globba, Hedychium and Kaempferia, the length varies between 0.1-5 cms. or the lamina may be sessile. Long petioles which reach up to 20 cms. or more in length are characteristic of Curcuma and Scaphochlamys, and the relative length of the petiole and lamina may be useful for specific separation

in these genera. Another characteristic of the genera with long petioles is that there is less distinction between the sheath and petiole as in Curcuma, Scaphochlamys and Boesenbergia. The sheath narrows gradually into the petiole and the base of the blade is indicated by the ligule.

The petiole of Zingiber is unique among other genera in the family, and it resembles those of Costaceae. The petiole is swollen and 'pulvinus-like' (fig. 3.J; Plate 2.A) and resembles the true petiole of the dicotyledons. This feature was first reported on Zingiber officinale by Tomlinson (1956), and he referred to it as anomalous because it has never been reported by earlier workers. This comment inspired the observations made on the living and herbarium materials for about twenty-seven out of about 80-90 species in the genus. The 'pulvinus-like' petiole is characteristic of twenty-six of the twenty-seven species examined. The exception was an epiphytic species, (B. 4875) collected from Sarawak (Borneo) in 1962 by Mr. B.L. Burtt. The field observations on this plant show that the leaves are pendulous and hang down from the top of tree branches over the river. This plant is exposed to sunlight passing through the open spaces over the river. The adaptation of the petiole to the supposed function of the pulvinus, i.e. that of orientation, of the blade to rays of sunlight under the forest canopy, may not be necessary in this plant, hence probably, the differences in the petiole anatomy.

The characteristic of the petiole is a valuable character for the preliminary identification of most species of Zingiber on the field. On the herbarium specimens, the petiole dries up and the swollen part gives a dull, 'mealy' appearance which makes it very easy to identify.

PLATE 2. PETIOLE MORPHOLOGY AND ANATOMY OF ZINGIBER

- A. Zingiber puberulum - 'pulvinus-like petiole ($\times \frac{1}{3}$)
- B. Z. puberulum - collenchymatous bundle sheath (\times c.600)

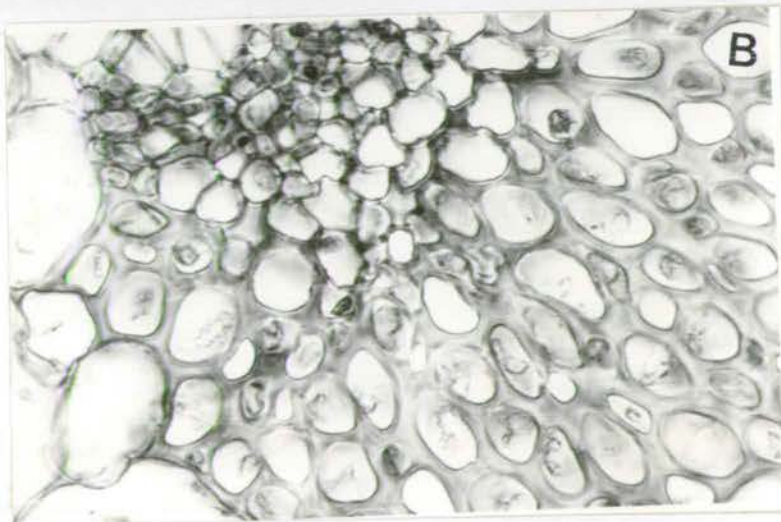


Plate 2

LAMINA.

There is great uniformity in the external morphology of the lamina in the Zingiberaceae and it provides very few characters that may be useful for generic delimitations. However, there are some variations in the shape, size and colour of the lamina in some genera and these may be of diagnostic importance at or below the species level.

In texture the lamina is usually thin or fairly thin. The lamina are held more or less horizontally in most genera whereas they are erect in Scaphochlamys, Curcuma, Boesenbergia, Cyphostigma, Kaempferia rotunda, K. ovalifolia and Cienkowskyia (African Kaempferia).

The upper surface of the leaves of Kaempferia are often variegated in both wild and cultivated materials (Plate 1.C), except in K. angustifolia and probably all the species of African Kaempferias (Cienkowskyia). The leaves of Alpinia sandarac are similarly variegated.

The variegation on the leaves of Kaempferia is probably produced in the same way as those on the leaves of Marantaceae as was described by Tomlinson (1961, 1969). However, the variegation on the leaves of Kaempferia gilbertii and Alpinia sandarac may possibly be due to sectorial chimaeras. Further investigation is needed to elucidate the formation of this variegation.

One major difficulty to the use of differences in colour of the lamina is that most of the colours are lost in dried specimens, and living specimens are always needed. Therefore, the differences in the colour of some species have not been considered in any detail here.

The lamina varies in size from species to species and even so from the base to the top of a plant. The smallest leaves are probably those of Roscoeia minuta where they reach up to 7 cm. long by 2.5 - 3 cm. broad.

Whereas the leaves may reach up to 6-110 cms. long by 10-20(25) cms. broad in most genera in the tribe Alpinieae.

The lamina varies in shape and may be elliptic, oblong, lanceolate, ovate as in most species or orbicular as in Kaempferia, Scaphochlamys. The margin of the lamina is translucent in some genera and entire except where there may be bristles on it as in Aframomum and Alpinia. The base may be attenuate, cuneate, round, auriculate or cordate as in Globba winittii and Camptandra latifolia.

The leaf venation is a parallel monocotyledonous type, the primary longitudinal veins develop from the midrib and run into a marginal commissure at a variable distance and angle along the margins. The veins nearer the upper one-third of the blade may run into an apical commissure. The primary veins are widely spaced and the smaller ones less conspicuous on the abaxial surface of Kaempferia, Curcuma, Scaphochlamys, Boesenbergia. The distance between the veins in these genera varies between 0.1-2.5 (3) mm. In the Globbeae, Alpinieae and some genera of Hedychieae, the primary veins are close together, and conspicuous although they do not always produce profound ribbing on the abaxial surface of the lamina. The distance between these veins varies between 0.1-0.7 mm. and rarely more than 1 mm. The distances between the primary veins on the abaxial surface of the lamina may be a valuable character, along with others, for the separation of some species within a genus as was done for Aframomum (Hepper 1968).

INDUMENTUM.

According to Tomlinson (1956), it is true that the distribution of the indumentum on any one species is very irregular, but the indumentum on the lamina may be useful for specific separation within a genus. The hairs

may be present on both or either surface, on the midrib, along the veins or on the margins alone. Hairs may be present at the base or the apex. The presence or absence of hairs, and the position where they are found on the lamina are diagnostic for each species or sub-species in a genus.

Although most species in this family are never conspicuously pubescent, completely glabrous blades are rare. Some of the hairs are microscopic and not easily observable by using the hand lens. However, the lamina of some species are densely pubescent and may be described by the common qualitative terms. They range from velutinous as on the abaxial surface of the lamina of Cenolophon sp. and Zingiber sp. (Lace 5245), villose as on Hornstedtia villosa to strigose or scabrous as on both surfaces of the lamina of most species in Globba. The anatomical features of these hairs are dealt with on page 74.

B. ANATOMICAL CHARACTERS

THE RHIZOME

The observations made from the transverse sections of the rhizome show that the anatomy of this organ is similar in all the species examined. The rhizome consists of the following layers; the periderm, cortex, endodermis, pericycle, stele and central pith.

The periderm is composed of about three to eight rows of cells. The inner layers may consist of thin-walled cells which are arranged in parallel or storied series referred to as the 'etagen' type (Tomlinson 1956). The cells in this zone divide anticlinally in the manner similar to the phellogen cells in the dicotyledons, although there are no such organised phellogen cells observed. The periderm cells are usually suberized but occasionally they may not become suberized, and according to Tomlinson (1956), the suberized cells may alternate in parallel series with the unsuberized cells as in Kaempferia angustifolia. In some rhizomes, e.g. Zingiber officinale, the periderm cells are internal to parenchyma cells which are not arranged in parallel series as in the periderm. Also, the periderm may not be developed in the rhizome of some species and according to Tomlinson (1956), the development of the periderm appears to be associated with the ecological differences between species since it is not present in all the individuals of the same species. In the Alpinieae, the periderm in some species may consist of thick-walled cells or fibres where the rhizomes are woody, e.g. Elettaria. The cortex is usually inside and may take up to one-third to one-half of the entire diameter of the rhizome. The cells of the cortex are usually larger and with abundant air spaces in between them. In most species,

abundant starch grains and tanniniferous cells are found in the cortical cells. Because of the transitional position of the rhizome between the aerial stem and root, many of the vascular bundles run obliquely and in various directions, and some others anastomose longitudinally.

The cortex is separated from the central cylinder by the endodermis. This feature is not present in the aerial stem. The cells of the endodermis are thin-walled and the casparian thickening in the radial walls may be less distinct than it is in the root. The vascular elements are arranged very close to the endodermis and sometimes they may be less differentiated as distinct bundles. The central cylinder consists of numerous scattered bundles which usually contain one xylem element. The bundle sheath is composed of thin-walled fibres but occasionally this may be replaced by paranchyma cells.

THE ROOT.

In the root, periderm is not developed as in the rhizome, but cells in the piliferous layer may be arranged in a similar pattern to the periderm. The root as seen from transverse sections, consists of the piliferous layer (exodermis), cortex, endodermis, pericycle, stele and pith. (fig. 4.a-g).

The epidermis of the root is made up of medium-sized parenchyma cells. These cells appear slightly papillate in most species, e.g. Kaempferia rotunda (fig. 4.b) and Hornstedtia scyphifera (fig. 4.d). The walls of the cells are usually thin, but the external tangential and radial walls are thickened in Hornstedtia scyphifera (fig. 4.d) and some species in Elettaria.

The root hairs are usually simple, but branched hairs were observed on the root of Kaempferia rotunda (fig. 4.b), Hedychium gardnerianum and H.

x Raffillii. The piliferous layer may be composed of parenchyma cells which are usually tightly compacted and with thin walls (fig. 4.b,c) or fibres or fibre-like cells with moderately thickened walls as in Scaphochlamys rubromaculata (fig. 4.b). These fibres form a narrow cylinder in the exodermis of most species and may consist of more thickened fibres as in Scaphochlamys and most species of the tribe Alpinieae, (fig. 4.d,e).

The cortex of most genera particularly in the tribes Globbeae, Hedychieae and Zingiber (Zingibereae) are composed of parenchyma cells with thin walls. But the outer cortex may be made up of thick-walled fibres which may spread from the exodermis to most parts of the inner cortex, as in most species of Scaphochlamys and a number of species in the tribe Alpinieae. The remaining part of the inner cortex is usually composed of large parenchyma cells. The presence of the fibrous cylinder in the exodermis and frequently in the cortex of Scaphochlamys may be a useful diagnostic character for this genus since such fibrous cylinder is absent from the cortex of the other genera in the Globbeae, Hedychieae and Zingiber. The fibrous cylinder which may be present in the exodermis of these tribes, is usually composed of thin-walled fibres and these are different from the thick-walled fibres in Scaphochlamys.

The endodermis is made up of one row of cells which usually show the U-shaped thickening characteristic of the monocotyledons (fig. 4.f). In some species however, e.g. Zingiber mollis, the endodermis is not well thickened and it is recognisable only by the characteristic casparian thickening on the radial walls of the cells.

The pericycle is represented by one layer of unthickened cells immediately inside the endodermis. The two-layered pericycle reported by Solereder &

FIG. 4. TRANSVERSE SECTIONS THROUGH THE ROOT.

Explanation in the text.

- a. Hedychium gardnerianum (x 15)
- b. Kaempferia rotunda (x c.180)
- c. Scaphochlamys Kunstleri (x c.180)
- d. S. rubromaculata (x 31)
- e. S. rubromaculata (x c.680)
- f. Amomum cardamomum (x680)
- g. Hornstedtia scyphifera (x680)

end. = endodermis.

fib.cy. = fibrous cylinder.

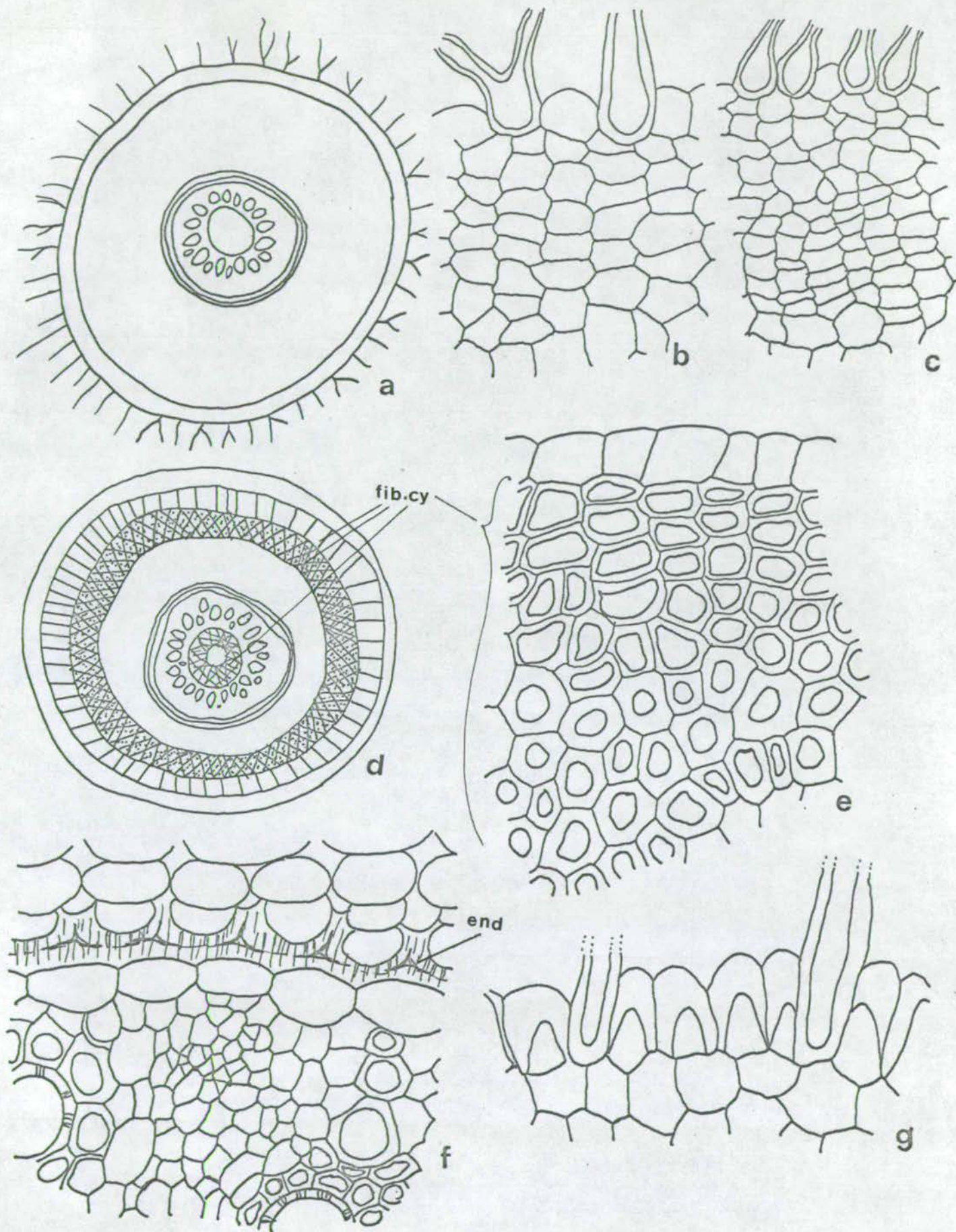


Fig. 4

Meyer (1930) was not observed in this study.

The vascular elements are surrounded by a ground tissue which is usually consisted of fibre-like cells with thickened and un lignified walls. In some species, e.g. Scaphochlamys rubro-maculata the fibres of the ground tissue may be greatly thickened. Moreover, an internal fibrous cylinder, which is almost similar to those of the cortex, may surround the pith (fig. 4.d). The central pith, which is characteristic of monocotyledons, is present in all the roots examined. It consists of rounded and thin-walled parenchyma cells with intercellular spaces in between them.

The roots are polyarch and the vascular bundles are arranged radially with the protoxylem poles close to the pericycle and the metaxylem towards the pith. The phloem elements occupy the position close to the pericycle and in between the adjacent xylem elements. In some cases, they may extend radially towards the centre of the root as in Brachychilum horsfieldii and H. gardnerianum, and also, isolated phloem elements are found sometimes inside the fibrous ground tissue as in Anomum sp. (B. 2477).

T.S. STEM (INTERNODE).

The true stem (internode) is normally covered by leaf sheaths which wrap round it in concentric circles. The epidermis is similar to those of the sheath and petiole. The cells are narrow and usually smaller than those in the internal ground tissue. These cells vary much in size but the width is frequently wider than the depth. A thin cuticle covers the external wall of the cells. The cell walls are thin except in some cases, e.g. Hornstedtia, Elettaria and Riedelia, where the external walls may be slightly thickened. Cortex. The width of the cortex varies from species to species. In the

genera with a well-developed true stem, the width may be from about one-eighth to one quarter that of the central cylinder (fig. 5.A-D). It is generally wider in those genera with a short stem, as in Boesenbergia (fig. 4.D), Kaempferia and Curcuma.

The ground tissue of the cortex is composed of parenchyma cells which vary in size from the smallest near the epidermis to the large cells towards the fibrous cylinder. Intercellular spaces are usually present and assimilating tissue may be represented by rounded cells which contain few chloroplasts and starch grains.

Large and small vascular bundles are distributed in the ground tissue of the cortex where they form a system of irregular rings (fig. 5.A). The number of rings varies from species to species and at different levels on a plant. Generally, there are from about three to five rings in most genera, as in Alpinia sanderar (fig. 4.A). One or two rings are characteristic of Globba (fig. 4.B), Caulokaempferia, Camptandra and Roscoe. In Riedelia, Hornstedtia and Geostachys, the vascular bundles may be congested to form a mechanical zone in the cortex. The cortical bundles are usually very conspicuous, their bundle sheaths being more massive than those of the central cylinder (fig. 4.E,F). These bundle sheaths are composed of sclerenchymatous fibres which are variable in thickness. The bundle sheaths, of some of the vascular bundles in the genera with short stems, e.g. Boesenbergia, Curcuma, Kaempferia, may be collenchymatous. The transverse sections through the stems of these genera were taken from the short stem, which is usually close to the rhizome and an area where growth is very active.

The bundle sheath is usually complete around the vascular bundles or it may be wider near the xylem than the phloem (fig. 5.E,F). In some cases it

FIG. 5. TRANSVERSE SECTIONS THROUGH THE TRUE STEM AND RHIZOME.

Explanation in the text.

- A. Alpinia sandarac (x 15)
- B. Globba atrosanguinea (x 15)
- C. G. atrosanguinea - t.s. inflorescence axis (x 31)
- D. Boesenbergia sp. (B & M 5164). T.S. rhizome (x 15)
- E. Alpinia mutica - Cortical v. bundle (x 180)
- F. Globba winitii - Cortical v. bundle (x 180)

fib. cy = fibrous cylinder.

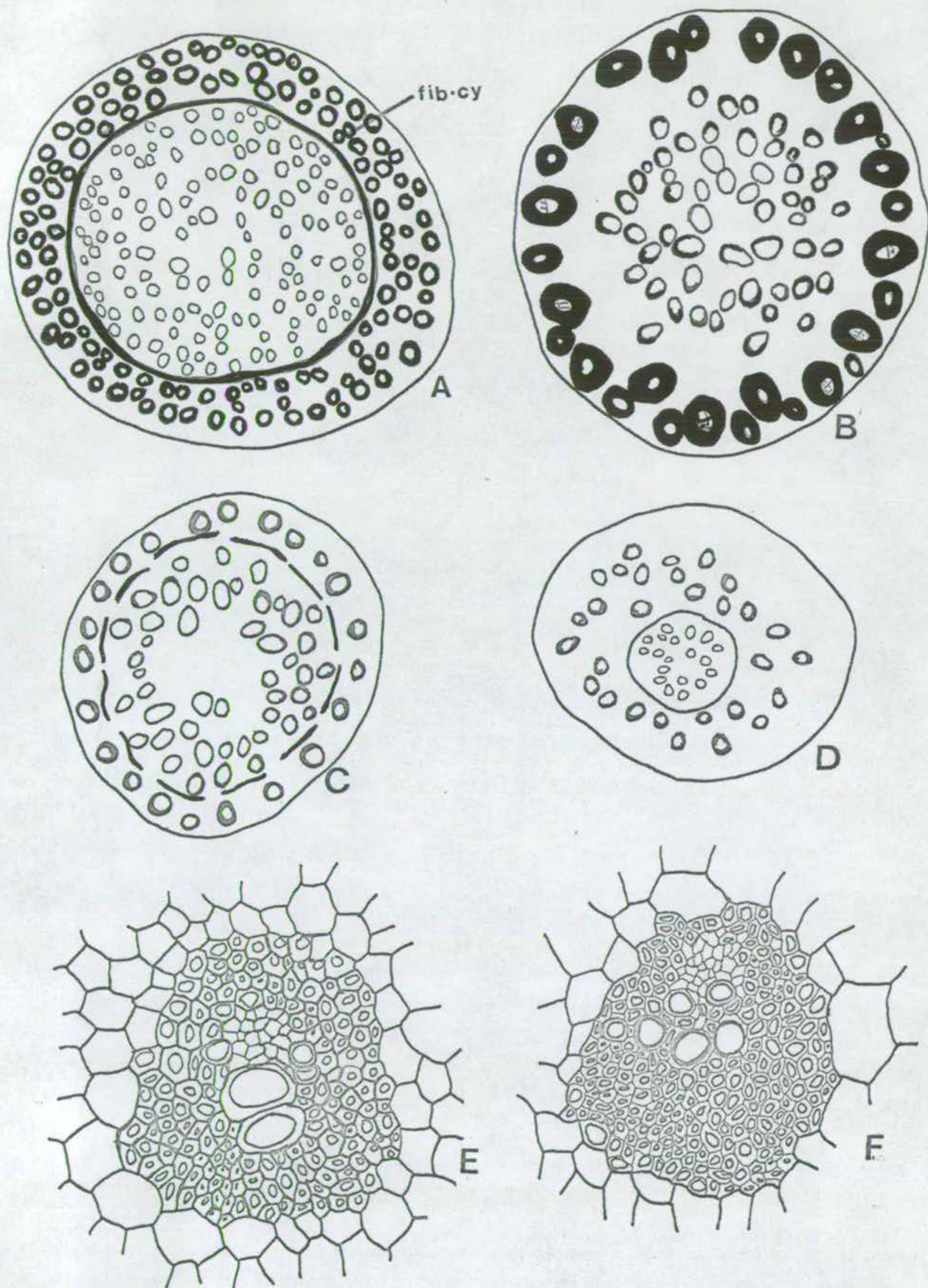


Fig-5

may be separated into two arcs by some parenchyma cells or thin-walled fibres. The xylem elements with few smaller ones, as in Alpinia mutica (fig. 5.E), or several smaller ones as in Globba winittii (fig. 5.F). The phloem consists of sieve tubes and phloem parenchyma. The phloem is separated from the xylem by a group of parenchyma cells.

Fibrous cylinder. A fibrous cylinder (fig. 5.A) separates the cortex from the central cylinder. This fibrous cylinder is composed of sclerenchymatous fibres which are similar to those of the bundle sheaths. The cylinder varies in thickness from species to species, but in most cases may be between three to five cells thick. The thickness of its constituent fibres also varies. In those genera where the cylinder is well developed as in Hornstedtia, the fibres may be very thick, whereas where it is feebly developed it may be represented by parenchyma or prosenchymatous cells, as in Phaeomeria magnifica.

A fibrous cylinder is present in most genera except Globba (fig. 5.B), Caulokaempferia and Mantisia wardii. In the case of Globba and Mantisia wardii, although the fibrous cylinder is absent from the part of the stem between the base and the level of the second leaf to the top of the plant, it may be developed in the inflorescence axis (fig. 5.C). The transverse sections of the stem show the presence of isolated fibrous strands at the level of the second leaf from the top of the plant. These fibrous strands are further differentiated in the inflorescence axis where they form a complete fibrous cylinder. The fibrous cylinder may be feebly developed or absent in Scaphochlamys, Curcuma, Kaempferia and some species of Boesenbergia where the true stem is short and it may be present in the inflorescence when the latter is produced.

It might have been plausible to correlate the absence of the fibrous cylinder with the dwarf habit of the genera mentioned above, but this cylinder is developed invariably in the inflorescence axis to support the weight of the flowers, as is obvious in Globba.

The fibrous cylinder, in this family, is usually separate from the vascular bundles, i.e. not frequently fluted as in the Costaceae.

Central cylinder. The ground tissue of the central cylinder is composed of large parenchyma cells with occasional intercellular spaces between them. The walls of these cells are thin. Smaller vascular bundles than those in the cortex are scattered in the ground tissue. The bundle sheaths are less strongly differentiated and are usually separated by parenchyma cells into outer and inner caps. The outer caps may consist of thin-walled parenchyma cells or the entire sheath may be composed of parenchymatous cells.

SHEATH AND PETIOLE ANATOMY.

EPIDERMIS - SURFACE VIEW.

The abaxial epidermis of the sheath and petiole is usually differentiated into costal and intercostal areas. This is the case whether the surface of sheath and petiole is striated or smooth. The costal cells are rectangular, except in some species, e.g. Burbridgea pubescens, where they are transversely stretched. They are usually narrow and many times longer than broad. The cell walls may be thin or fairly thickened and with simple pits, as in Amomum repoense, Elettaria surculosa and Geostachys taipingensis.

The intercostal cells may be rectangular and as long as the costal cells, but they are usually wider and slightly stretched transversely. The walls are thin or moderately thickened. It is true, as reported by Tomlinson (1956), that the hairs, oil cells and stomata are restricted to the intercostal

areas, i.e. furrows, on the sheath and petiole. This is usually the case particularly with the internal sheaths which are shielded by the overwrapping external sheath, or sheaths.

In some species of Hedychium, e.g. H. gardnerianum, the epidermis of the sheath and petiole is punctuated by pits. These were probably produced as a result of the disorganisation of some of the stomata on these organs. The pits are filled with some granular powdery substance which is dusted on the surface of the sheath in some species of Hedychium.

The adaxial epidermis is usually not well differentiated into costal and intercostal areas. The epidermal cells are usually transversely stretched. The walls of the adaxial epidermal cells of the sheath are thin and never strongly thickened.

TRANSVERSE SECTIONS.

Abaxial epidermis. Generally, the cuticle over the abaxial epidermis is thin except in some species where it may be slightly thickened, as in Alpinia subverticillata (fig. 10.b), Riedelia sp. The epidermis, as seen from transverse sections, is usually narrow and the shape of the cells may be either rectangular or square. The walls are not usually thickened except in few cases, such as in Hitchenia careyana (fig. 10.c), Alpinia subverticillata and Hornstedtia leonurus.

Adaxial epidermis. The adaxial epidermal cells of the sheath are neither thickened nor sclerotic. The cells are compressed over the similarly flattened sub-epidermal cells and these resemble an epithelium. The adaxial epidermal cells of the petiole of the tribes Globbeae, Hedychieae, Zingiber and few genera in the Alpinieae, e.g. Phaeomeria, are usually thin-walled. But in the majority of the other genera, the adaxial cells may be

slightly thickened as in Alpinia subverticillata (fig. 10.b) and Achasma megalocheilos.

The sub-epidermal cells of the sheath and petiole may be thickened or sclerotic and may form a sclerotic zone. These sclerotic cells, if present, may be found on both or either of the abaxial and adaxial sub-epidermal layers of the petiole, as in Alpinia subverticillata (fig. 10.b), A. pahangensis, A. rufa, Achasma megalocheilos, Aframomum melegueta and Hornstedtia piminga. Such cells, when present in the sheath, occupy the abaxial sub-epidermal layers only, as in Renealmia occidentalis (fig. 10.a, d,e), and some species in Hornstedtia, Elettaria, Geostachys, Alpinia, Anomum and Achasma. The sclerotic cells are never confined to the adaxial surface of the sheath as suggested by Tomlinson (1956); in fact, they have not been observed in this position on the sheath of any of the materials examined for this study.

Ground tissue. The ground tissue of the sheath and petiole is composed mainly of large parenchymatous cells. The layers of cells nearer the epidermis may be sclerotic, as has been discussed above. Apart from these, the cells are thin-walled or moderately thickened.

VASCULAR BUNDLES.

The vascular bundles in the sheath and petiole have been grouped, for ease of reference, into four systems by Tomlinson (1956) on account of their size and position in these organs (fig. 6.A; 7.a). These are (i) main arc I, (ii) abaxial arc II, (iii) adaxial arc III, and this may be regrouped into two to include (iv) adaxial arc IV.

There are some variations in the degree of development of the vascular bundles at the different levels on a plant. The main arc I bundles are

FIG. 6. TRANSVERSE SECTIONS THROUGH THE LEAF SHEATHS.

Explanations in the text.

- a. Alpinia mutica (x 15)
- b. A. mutica (x 15)
- c. & d. Roscoeia auriculata (x 15)
- e. Kaempferia aethiopica (= Cienkowskya aethiopica) (x 31)
- f. Caulokaempferia linearis (x 62)
- g. Boesenbergia sp. (B & M 5164) (x 31)

exp.c = expansion cells; o.c = oil cells.

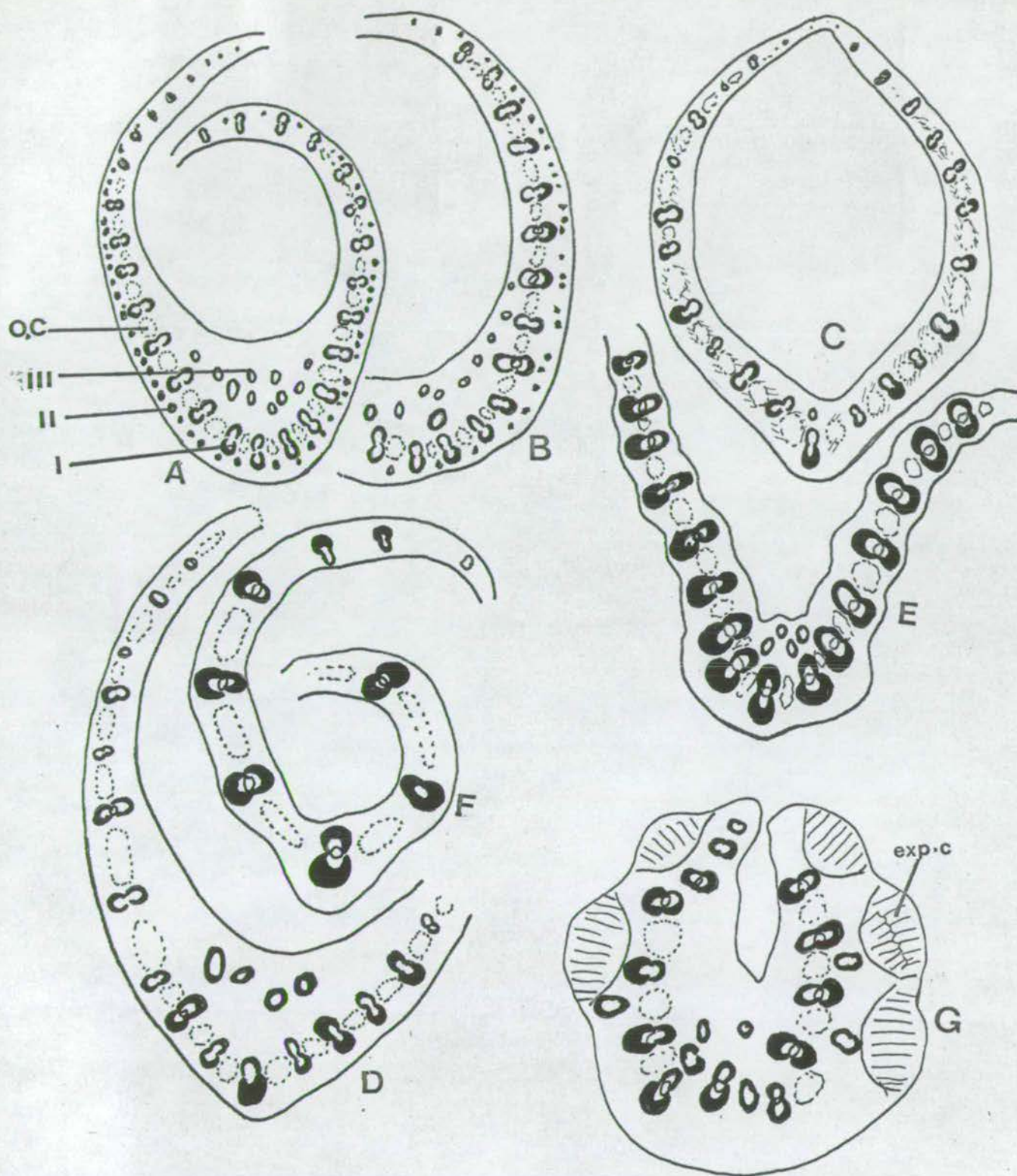


Fig-6

well developed at all levels up to the midrib of the lamina. Arc II bundles are also well developed in the sheath and petiole of most genera. They are, however, absent from the abaxial position in the sheath of Roscoea (fig. 6.C), Cienkowskya (African kaempferias) (fig. 6.E) and Caulokaempferia (fig. 6.F). Although arc II bundles are absent from the abaxial position in Roscoea, similar subsidiary vascular bundles are present but pectinate with the main arc I vascular bundles and air canals in the sheath. This arrangement is characteristic of all the species of Roscoea. Arc II vascular bundles may be present in the sheath of some species of Kaempferia, e.g. K. rotunda, K. pulchra, and K. elegans, but absent in K. gilbertii and K. angustifolia. This situation does not make the presence or absence of the arc II vascular bundles a useful character distinguishing between the Asiatic and African Kaempferias.

Arc II bundles are usually present in the petioles of the tribes Globbeae (fig. 7.b), Hedychieae (although it may be represented by a few bundles as in the Scaphochlamys, Kaempferia and Curcuma (fig. 7.c), numerous in Hedychium (fig. 7.d) and Brachychilum), Zingiber (Zingiberaceae) and Cyphostigma; and some species of Alpinia, Amomum, Aframomum, Rhynchanthus, Elettaria and all the species of Renealmia. Arc II bundles are either few or absent in the rest of the genera or species of the tribe Alpinieae as in Elettaria (fig. 7.f) and Alpinia pahangensis (fig. 7.g).

Arc III bundles are present in the upper part of the sheath, and this arc reaches its maximum development in the petiole of the genera in the Globbeae (fig. 7.b) and Alpinieae (fig. 7.f). It is represented in the petioles of the Hedychieae by few large bundles (fig. 7.c), except in Hedychium (fig. 7.d) and Brachychilum, where the bundles are smaller and

FIG. 7. TRANSVERSE SECTIONS THROUGH THE PETIOLE.

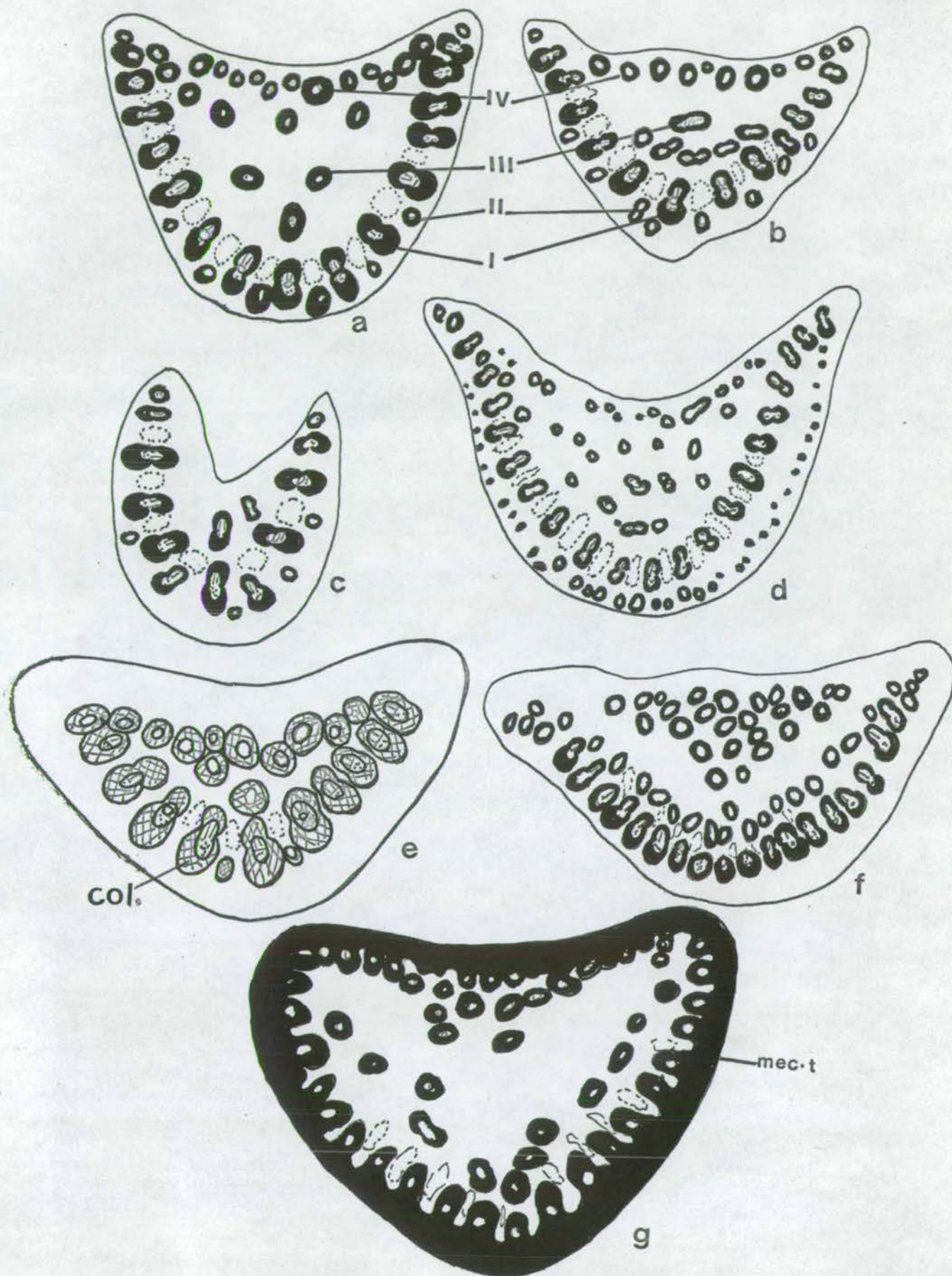
Explanation in the text.

- a. Aframomum melegueta (x 31)
- b. Globba atrosanguinea (x 15)
- c. Curcuma longa (x 15)
- d. Hedychium thyrsiforme (x 31)
- e. Zingiber officinale (x 31)
- f. Elettaria surculosa (x 31)
- g. Alpinia pahangensis (x 62)

mec.t = mechanical tissue

col. = collenchymatous bundle sheath

Fig.7



numerous.

Arc IV is also well developed in the petiole and where there are many vascular bundles belonging to both arc III and IV, arc IV may not be easily distinguishable. The pattern of arrangement of the arc IV bundles may be distinct and characteristic of a genus or group of genera as in Globba, Elettaria, Achasma and some species of Alpinia. In Globba there is usually an adaxial row of vascular bundles which are very close to the adaxial epidermis (fig. 7.b). This pattern is characteristic of Globba. The vascular bundles in the petiole of Zingiber (fig. 7.e) are arranged together in a median position and air canals are either absent or poorly developed between them. In Elettaria, the arcs III and IV bundles are arranged close together in a median position in the petiole (fig. 7.f). This pattern appears like an 'inverted triangle' in the median area and quite separate from the row of arc III bundles which run parallel and close to the main arc I bundles. This type of arrangement is also common among species of Achasma and to some extent in some species of Alpinia, such as in A. blepharocalyx and A. graminacea. Arc IV bundles are generally few or absent in the genera with canaliculate petioles (fig. 7.c), such as Curcuma, Scaphochlamys, Camptandra, Kaempferia and Boesenbergia. Although the petioles of Zingiber are not always channelled, arc II bundles are absent from them. The 'pulvinus' nature of these may be the reason why extra strengthening tissue is not required in the adaxial side of the petiole.

PETIOLE ANATOMY OF ZINGIBER.

The petiole of the genus Zingiber is unique anatomically as it is in morphological features. Tomlinson (1956) discussed this uniqueness to some extent, and the following is more or less an elaboration of the same feature

because it appears to be a useful taxonomic character for this genus.

The vascular bundles in the petioles of most genera in the family, except Zingiber, are usually sheathed by an inner bundle sheath which is composed of sclerenchymatous fibres. The transverse sections of the part of the petiole of Zingiber, which appear externally as a 'pulvinus', show that the bundle sheath in this area is made up of collenchymatous cells (fig. 7.e; 8, Plate 2.B). This collenchymatous bundle sheath was first reported by Tomlinson (1956) on Zingiber officinale, and he later observed the same for Z. puberulum Tomlinson (1969). He referred to this bundle sheath as 'anomalous' because it has never been reported by previous workers in this family. This comment inspired the detailed observation made on the materials for about twenty-seven species out of about 80-90 species in the genus (Willis 1966), that were available for this study. It is very interesting to note that this collenchymatous bundle sheath was observed in all but one species. The exceptional species is an epiphytic species, as discussed on page 25, and its petiole bundle sheath is composed of thick sclerenchymatous fibres instead of the collenchymatous cells characteristic of the other species. The anatomical features of this species, particularly those of the petiole, have evidently varied in response to changes in the habit and habitat of the epiphytic species. Actually, the pendulous habit of the leaves of this species might call for a stronger strengthening tissue to be developed for withstanding the constant force of the wind in the open environment above the rivers in which these plants abound (Mr. B.L. Burt - private discussion).

Moreover, certain petiolar features are associated with the 'pulvinus' of Zingiber, such as the reduction in the development of the air canal and

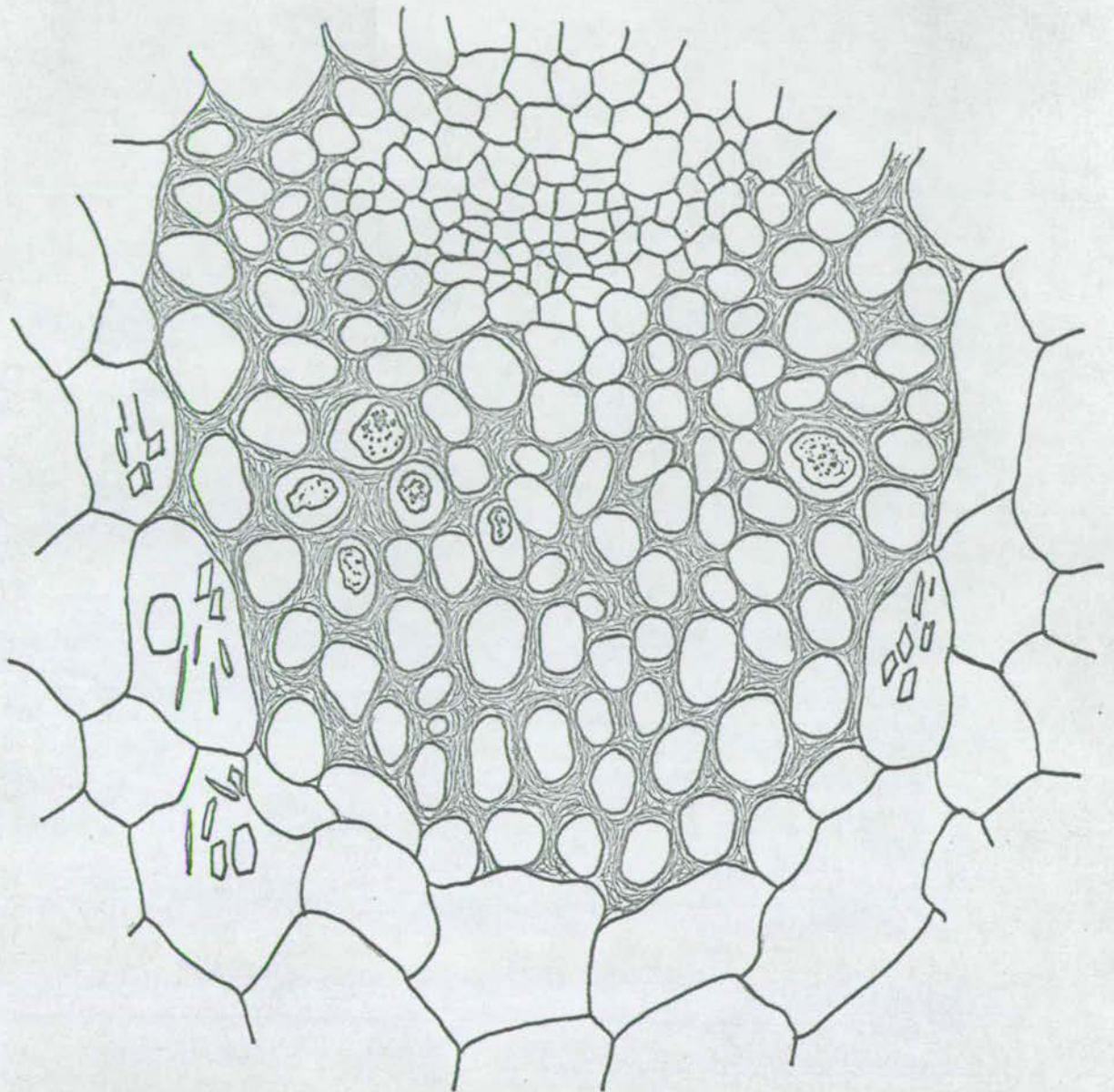


Fig. 8

FIG. 8. PETIOLE ANATOMY OF ZINGIBER.

Detail of Collenchymatous bundle sheath.

(x 680).



assimilating tissue, and the hypertrophy of the ground parenchyma cells within the 'pulvinus'.

Generally, collenchymatous cells are associated with those areas on a plant which are subjected to constant movement, stress, and where growth might not have been completed. In the Zingiberaceae, collenchymatous cells are not uncommon in the bundle sheaths of the vascular bundles in the rhizome, and particularly in the swollen stem base and the transitional area between the stem and rhizome. Also, collenchymatous cells may be present in the sub-epidermal layers at the junction between the ligule and sheath. The presence of these cells in the petiole of Zingiber is a distinct morphological and anatomical character, and it recalls the function of the pulvinus in the dicotyledons. The primary function of the pulvinus is that of the orientation of the leaves to the rays of sunlight. The Zingiber plants living as they do under the rain forest, it is not surprising that this rather primitive character is retained to enable the plants to trap sufficient energy from the constantly reduced beams of sunlight which pass through the forest canopy.

Although the number of species examined here is just slightly more than one-quarter of the total known for the genus, the collenchymatous bundle sheath is no doubt a diagnostic character for Zingiber, particularly since such is not present in the remaining genera of the Zingiberaceae. The taxonomic significance and relationship of this character is discussed on page 179.

MECHANICAL TISSUE.

The vascular bundles and their sheaths are the primary strengthening tissues of the monocotyledonous plants. Extra strengthening tissues, in the form of mechanical tissues, are developed occasionally, and these have been

observed in a number of genera in the Zingiberaceae. Table 2 shows the genera and species where these tissues have been observed.

As far as could be determined, except for the adaxial sclerized sub-epidermal cells observed by Tomlinson (1956) in the petiole and midrib of Alpinia javanica and Hornstedtia conica, there is no information in the literature concerning the occurrence of this tissue in any member of the family. However, such tissues have been reported for Marantaceae, Heliconiaceae and Strelitziaceae (Tomlinson 1969). The comparison of the observations made in this study with those by Tomlinson (1956,69) shows that these mechanical tissues are well developed in both the wild and glasshouse cultivated specimens. This is contrary to the common belief that certain characters which occur in the wild specimens, such as stegnata, mechanical tissue and hypodermal fibres, might not be equally developed in the cultivated specimens. As far as this study is concerned, mature living herbarium material of both wild and cultivated specimens were observed in detail, and it is very interesting to note that both show the presence of the mechanical tissue. Younger plants might not give the same results.

In the sheath, the mechanical tissue may be produced in a number of closely similar ways, depending on the position where the tissue is found in relation to the abaxial epidermis, and also the type of tissues which contribute to its formation:

- (i) The abaxial subsidiary (arc II) vascular bundles may be numerous, large or small, and congested. They may be pectinated by many solid fibrous strands to form a rather disjointed mechanical tissue. Examples are found in Hornstedtia pininga (fig. 9.a), Adelmeria bifida (fig. 9.b), Alpinia penduliflora (fig. 9.c), A. publiflora, A. brevilabris, Anomum pierceanum

TABLE 2: MECHANICAL TISSUE IN THE SHEATH AND PETIOLE

	SPECIES	SHEATH		PETIOLE	
		abaxial	adaxial	abaxial	adaxial
1	<u>Amomum hewithii</u>	+	-		
2	<u>A. ovoideum</u>	+	-	+	-
3	<u>A. pierreanum</u>	+	-	-	-
4	<u>A. sp. (B 5337)</u>	+	-	+	-
5	<u>A. sp. (B 5277)</u>	+	-	-	-
6	<u>A. sp. (5303)</u>	+	-	-	-
7	<u>A. trilobium</u>	+	-	+	-
8	<u>Aframomum humburgii</u>	+	-	-	-
9	<u>A. luteo-album</u>	+	-	-	-
10	<u>Alpinia rufa</u>	+	-	+	+
11	<u>A. brevilabris</u>	+	-	-	-
12	<u>A. publiflora</u>	+	-	-	-
13	<u>A. allughas</u>	+	-	+	-
14	<u>A. graminacea</u>	+	-	-	-
15	<u>A. oxymitra (Cenolophon oxymitrum)</u>	+	-	-	-
16	<u>A. elegans</u>	+	-	-	-
17	<u>A. conchigera</u>	+	-	+	-
18	<u>A. formosana</u>	+	-	-	-
19	<u>A. penduliflora</u>	+	-	-	-
20	<u>A. latilabre</u>	+	-	-	-
21	<u>A. pahangensis</u>	+	-	+	+
22	<u>A. subverticillata</u>	+	-	+	-
23	<u>A. bracteata</u>	+	-	-	-
24	<u>A. calcarata</u>	+	-	+	-
25	<u>A. sp.</u>	+	-	+	-
26	<u>A. sp. (Score 2316)</u>	+	-	+	-
27	<u>A. sp. (Tsang 27121)</u>	+	-	-	-
28	<u>A. sp. (B 2268)</u>	+	-	-	-
29	<u>A. sp. (B 5166)</u>	+	-	-	-
30	<u>A. sp. (B 5300)</u>	+	-	-	-
31	<u>A. sp. (B 5289)</u>	+	-	-	-
32	<u>A. sp. (Tsang 29108)</u>	+	-	-	-
33	<u>Cyphostigma pedicellatum</u>	+	-	-	-
34	<u>Hitchenia careyana</u>	+	-	-	-
35	<u>Adalmeria bifida</u>	+	-	-	-
36	<u>Geocharis sp. (B 2869)</u>	+	-	-	-
37	<u>Geostachys taipingensis</u>	+	-	+	-
38	<u>G. sp. aff. penangensis (B 2827)</u>	+	-	+	-
39	<u>Rhynchanthus sp. (Keenan 3107)</u>	+	-	-	-
40	<u>Renealmia occidentalis</u>	+	-	-	-
41	<u>R. antillarum</u>	+	-	-	-
42	<u>R. bracteosa</u>	+	-	-	-
43	<u>Riedelia sp. (Millar 14594)</u>	+	-	+	-
44	<u>Elettaria surculosa</u>	+	-	-	-
45	<u>E. sp. (B 2085)</u>	+	-	-	-
46	<u>Elettaria sp. (B 5144)</u>	+	-	+	-
47	<u>E. sp. (B 4473)</u>	+	-	+	-
48	<u>Achasma sp. (B 2477)</u>	+	-	-	-
49	<u>A. sp. (B 5279)</u>	+	-	-	-
50	<u>A. sp. (B4721)</u>	+	-	-	-
51	<u>A. megalocheilos</u>	+	-	+	-
52	<u>A. subterranean</u>	+	-	-	-
53	<u>Hornstedtia scyphifera var. scyphifera</u>	+	-	-	-
54	<u>H. scyphifera var. fusiformis</u>	+	-	-	-
55	<u>H. philippinensis</u>	+	-	-	-
56	<u>H. leonurus</u>	+	-	+	+
57	<u>H. piminga</u>	+	-	+	+
58	<u>H. villosa</u>	+	-	-	-
59	<u>H. lophophora</u>	+	-	-	-
60	<u>H. reticulata</u>	+	-	-	-
61	<u>H. conoidea</u>	+	-	-	-
62	<u>H. microcheila</u>	+	-	-	-
63	<u>H. sp. (b 5051 and 5306)</u>	+	-	-	-

FIG. 9. TRANSVERSE SECTIONS THROUGH PART OF THE LEAF
SHEATHS SHOWING MECHANICAL TISSUE

Explanation in the text.

- a. Hornstedtia pininga (x 31)
- b. Adelmeria bifida (x 62)
- c. Alpinia penduliflora (x 62)
- d. Geostachys taipingensis (x 62)
- e. Hornstedtia scyphifera (x 62)
- f. H. conoidea (x 62)
- g. H. leonurus (x 31)
- h. Renealmia bracteosa (x 31)
- i. Achasma sp. (B 5279) (x 31)

m.t = mechanical tissue;
 scl = sclereids.

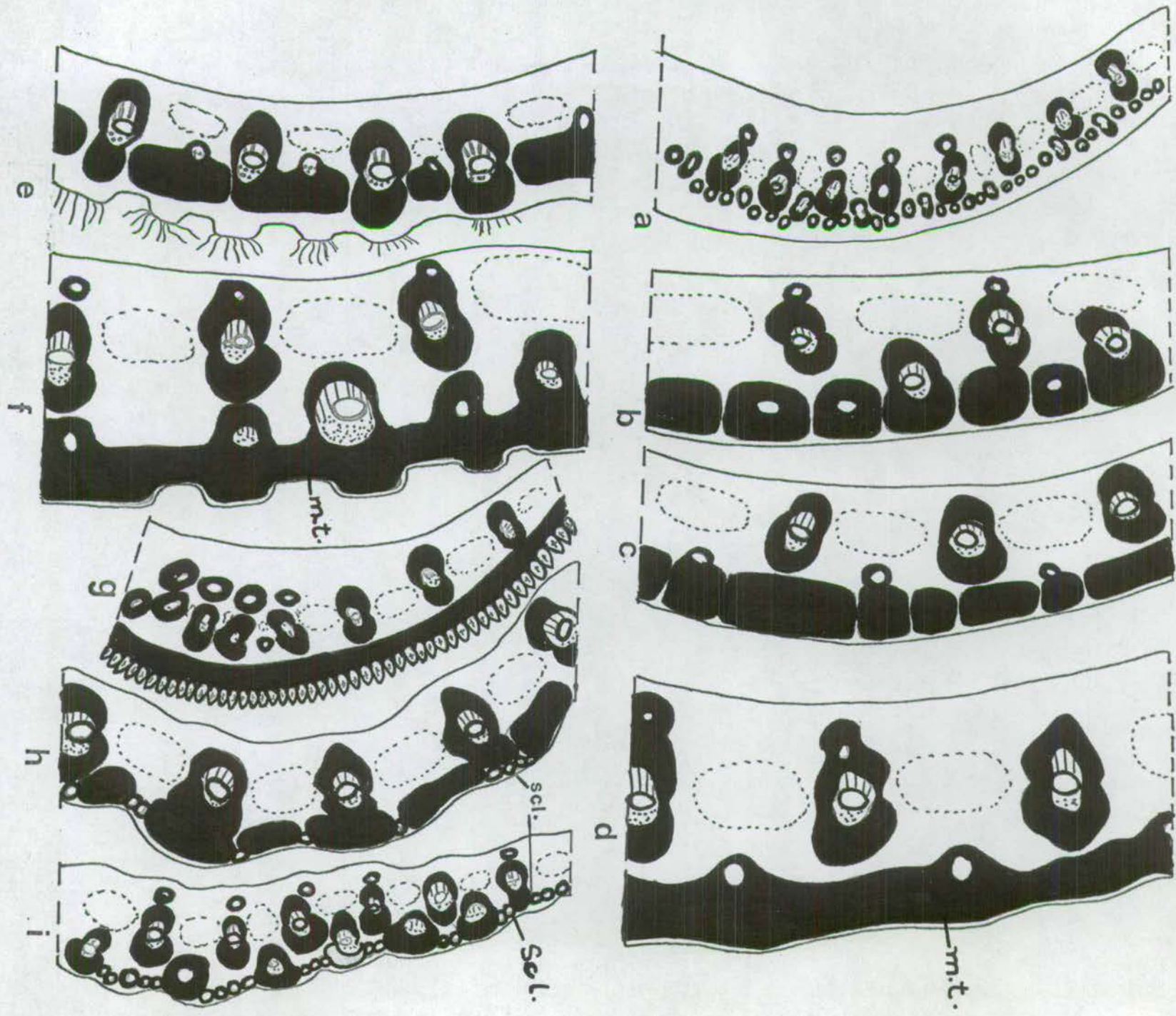


Fig. 9

and Achasma megalocheilos.

(ii) The bundle sheaths of the arc I and arc II vascular bundles may be massive and extended laterally to coalesce with each other and the adjacent fibrous strands to form a continuous mechanical tissue. Examples are: Geostachys taipingensis (fig. 9.d), Hornstedtia scyphifera (fig. 9.e) and H. villosa.

(iii) The spaces between the abaxial arc II bundles and fibrous blocks may be bridged by sclereids or sclerized cells to produce a fibrous tissue in the sheath. Examples are: Achasma sp. (fig. 9.h; Plate 3.E,F) and Renealmia bracteosa (fig. 9.i). Others are: Alpinia pulchra, Amomum hewithii, Renealmia antillarum and Elettaria surculosa.

(iv) A continuous fibrous tissue which is quite separate, or almost so, from either the arc I or arc II bundle sheaths, may be developed in the sheath. This may be composed entirely of, (a) sclerenchymatous fibres as in Hitchenia careyana, Hornstedtia conoidea (fig. 9.f; Plate 3.C), Amomum ovoideum, Aframomum humburgii, or (b) of sclereids and sclerized cells as in Hornstedtia leonurus (fig. 9.g), Amomum lepicarpa and Renealmia occidentalis (fig. 10.a).

The position of the mechanical tissue is probably a useful taxonomic character for specific separation, particularly in the genus Hornstedtia. This tissue may occupy a more or less median position very close to the arc I bundles and separated from the abaxial epidermis by some 5-10 cells in width as in Hornstedtia scyphifera (fig. 9.e), and H. villosa. The tissue may be close to the abaxial epidermis as in H. conoidea (fig. 9.f), H. macrocheila, H. lophophora and H. leonurus (fig. 9.g).

Mechanical tissue has been observed also in the petiole of some species

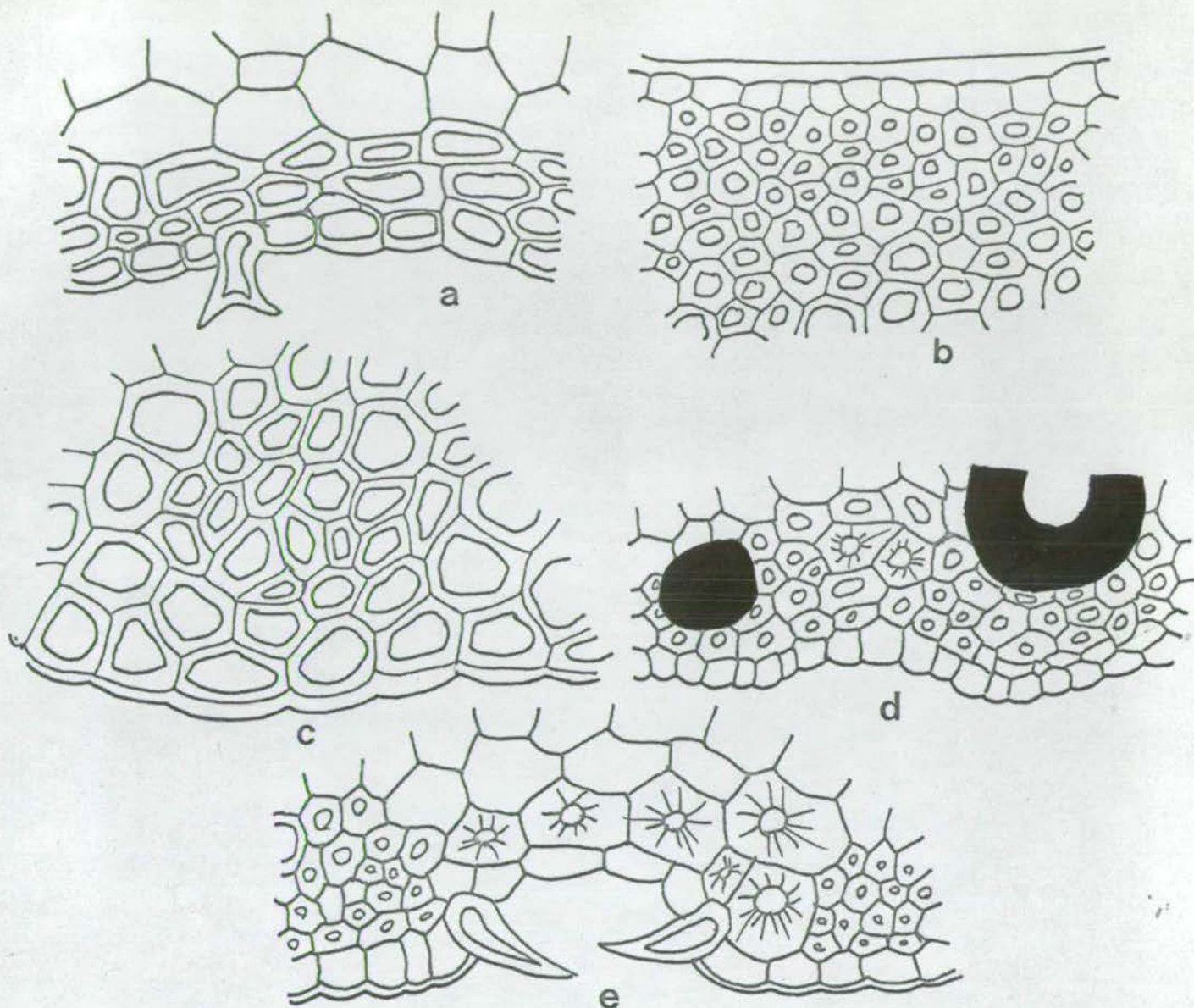


Fig.10

FIG.10. SCLEREIDS AND SCLEROTIC CELLS.

Explanation in the text.

- (a) Renealmia occidentalis - part of sheath:
- (b) Alpinia subverticillata - petiole adaxial tissue:
- (c) Hitchenia careyana - part of sheath:
- (d) Amonum lepicarpa - part of sheath:
- (e) Achasma sp. (B.5279) - sclereids from sheath.

All figures x c.180

PLATE 3. MECHANICAL TISSUE.

Explanation in the text.

- A. Aframomum humburgii (x c.160)
- B. Elettaria surculosa (x c.100)
- C. Hornstedtia conoidea (x c. 75)
- D. H. phillipinensis (x c.100)
- E. - F. Achasma sp. (B 5279) (x c.500)

E. x c.100) F. x c.650

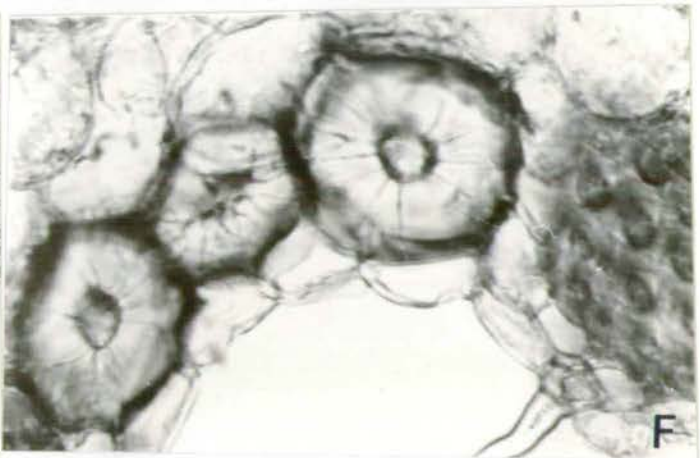
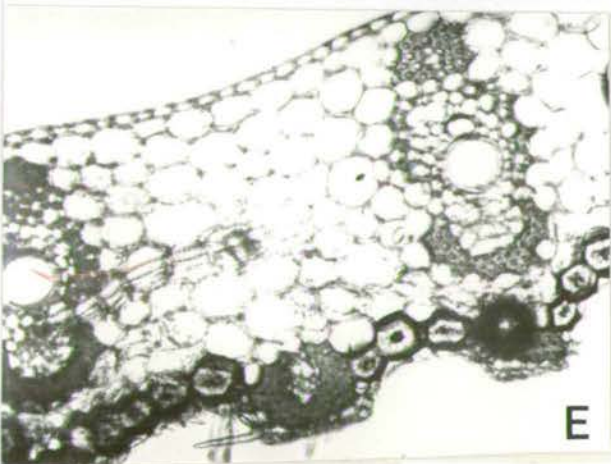
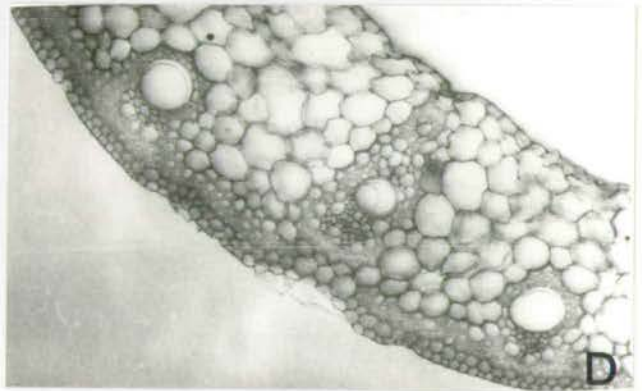
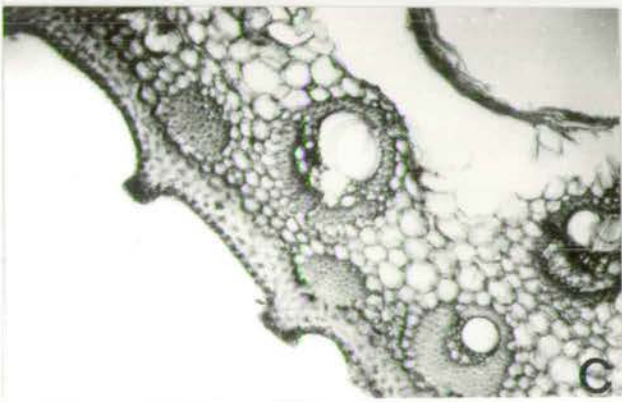
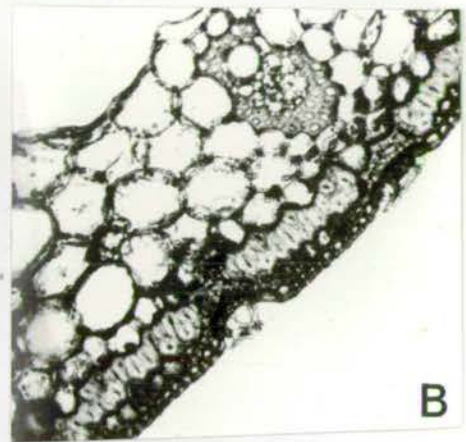
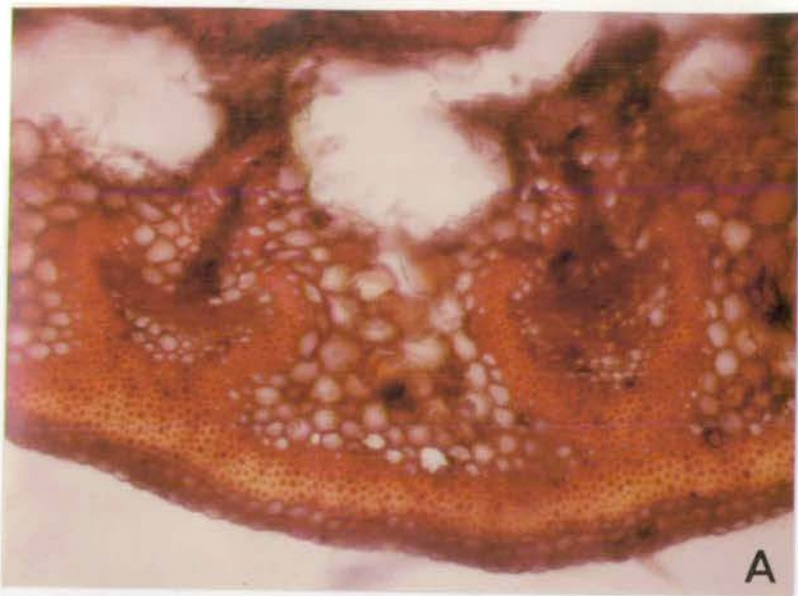


Plate 3

in the tribe Alpinieae. The tissue is usually produced either by the extension of the main arc I bundle sheaths and the subsequent coalescing of these as in Alpinia pahangensis (fig. 7.g) and A. conchigera or by sclereids and/or sclerenchymatous fibres as in Hornstedtia leonurus. Mechanical or sclerotic tissue may be present all round both the adaxial and abaxial sub-epidermal layers (fig. 7.g) or may occur on either abaxial or adaxial only, as in Aframomum humburgii (Plate 3.A) and Geostachys taipingensis.

Mechanical tissue is absent, except in Hitchenia careyana, from the members of the tribes Globbeae, Hedychieae and Zingiber (Zingibereae). But it has been observed in about 30-40% of the species and in about twelve out of thirteen genera of the tribe Alpinieae examined. The exception is the genus Phaeomeria and further investigation is needed on the remaining species of this genus not available for this study.

In most genera of the Alpinieae, the plants are tall, the leaves and inflorescence axis are large and heavy. The presence of the usually woody roots and rhizomes and the occurrence of extra mechanical tissue in the leaf axis might be essential as an additional strengthening tissue to support the weight of the plant organs, whereas such additional tissue might not be essential where the greater percentage of the plants are comparatively short as in the Globbeae, Hedychieae and Zingibereae.

ASSIMILATING TISSUE AND AIR CANAL SYSTEM.

A single row of air canals, which vary in size from the centre of the sheath and petiole to the margins (fig. 6.A-F; 7.a-g) is characteristic of this family. The air canals are also developed to some extent in the midrib of the lamina. These air canals are pectinated with the vascular bundles

of the main arc I in the abaxial half of the sheath and petiole. They are immersed in, or surrounded by, chlorenchymatous cells which contain chloroplasts. These canals are large and probably more developed in the sheath than in the petiole and midrib.

The single row of air canals system in the Zingiberaceae is comparable to those of the other families in the order Zingiberales and distinguishes this family from them.

Within the family there is some variation in the degree of development of the air canal system. According to Tomlinson (1956), these air canals are usually well developed in Kaempferia as they are in the other genera of the tribes Globbeae and Hedychieae. But the observation made by Tomlinson on Hornstedtia conica, concerning the reduction in the development of the air canals in the sheath of this species, might not be absolutely true of all other species in the genus. The species examined in this study show, like all other genera in the Alpinieae, that the air canal system is well developed at least in the sheath (fig. 9.a-1), whereas in the petioles of the tribe Alpinieae the air canals are developed, but because of the usually numerous vascular bundles, they are compressed and therefore smaller than those in the Hedychieae. The petiole of Zingiber is probably unique in that the air canals are poorly developed (fig. 7.a), and may be absent in some species. This is similar to the petioles of the Costaceae where the air canal system is poorly developed.

Expansion cells, which appear to be restricted in occurrence to the petioles and midribs, have been observed in the sheath of Boesenbergia sp. (B & M 5164) (fig. 6.g). This species is unique among all others in the presence of large hypertrophied cells which appear on the surface of the sheath and petioles as 'swellings' or 'bubblings' (fig. 1.0). In transverse sections,

these cells are elongated and colourless. They communicate with the outside environment through the stomata in the abaxial surface to which they are always close. It is difficult to link the function of rolling and unrolling of the lamina to these cells as was suggested, for those hypertrophied cells in the lamina,^{by} Tomlinson (1956, 69). It may be probable that they take part in the fluid exchanges between the organs and the outside environment.

LAMINA ANATOMY.

EPIDERMIS IN SURFACE VIEW.

MIDRIB: The epidermal cells over the midrib, as seen in the surface view, are usually rectangular or elliptic (fig. 11.a-d) in shape. They are similar to the epidermal cells on the sheath, petiole and costal cells of the lamina. The shape of the midrib cells is generally uniform for all the family, but two species of the same genus may differ in some details such as in shape and wall thickenings. In Roscoea and Kaempferia the midrib cells in surface view, are elliptic or more or less oval in shape. Those of Roscoea are papillate and are raised above the midrib as overlapping fish-scales (fig. 11.d), whereas these cells are less strongly papillate in Kaempferia. The reason why the midrib cells in Roscoea are more prominent in surface view might be because the midrib in transverse section shows a slightly protruding 'keel' (fig. 15.e,f) which carry the cells above.

The walls of the midrib cells vary in thickness from the thin-walled cells of Globba atrosanguinea (fig. 11.a), Roscoea (fig. 11.d), to the moderately thickened or thick-walled cells with simple pits as in Elettaria surculosa (fig. 11.b), Aframomum humburgii (fig. 11.c). This type is common in nearly all the species of the Alpinieae.

COSTAL AND INTERCOSTAL CELLS.

The epidermis of the lamina may be differentiated into costal cells (above the veins), and intercostal cells (in between the veins). These two areas are usually different from each other only in the shape and orientation of their cells. The epidermis of nearly all of the genera in the family, except Scaphochlamys, and to a less extent in Boesenbergia, Camptandra, are differentiated into costal and intercostal areas.

According to Tomlinson (1956) the modification of the cells above the veins depends upon the degree of buttressing of the veins and their sheaths on the lamina epidermises. Where the veins reach up to both or either of the two epidermises, the epidermal cells above the veins become modified and different from the adjacent intercostal cells. The veins reach up to the epidermises or hypodermises and the costal cells are frequently modified in the Globbeae, some genera of Hedychieae, and all the genera in Alpinieae, (to a less extent in Renealmia). In all these genera, the veins are conspicuously ribbed on the abaxial surface of the lamina. In Scaphochlamys, and some species of Boesenbergia, Camptandra, Kaempferia, where the veins do not always reach both or either epidermises, the costal cells are either not modified at all, as in the abaxial surface of Scaphochlamys or not strongly so as in Boesenbergia and some species of Camptandra and Kaempferia. The veins in the above genera are not conspicuously ribbed on the abaxial surface of the lamina but become more conspicuous on the adaxial surface as in Kaempferia and Curcuma.

The costal cells, where modified, are usually smaller and narrower than the adjacent intercostal cells. There is less variation in the costal cells and three closely similar types could be distinguished, depending upon their shape and orientation. They are:

- (1) The rectangular and/or square costal cells (fig. 11.e,f,h,i,j). These cells, as the name implies, are usually either many times longer than broad, or almost of equal length and breadth. The longer ones have their long axes parallel to the veins. Examples are: Zingiber officinale (fig. 11.e), Hornstedtia villosa (fig. 11.b) and Elettaria surculosa (fig. 11.h). In surface view, rectangular and square cells cannot be separated from each other,

FIG. 11. MIDRIB AND OTHER COSTAL CELLS.

Explanation in the text.

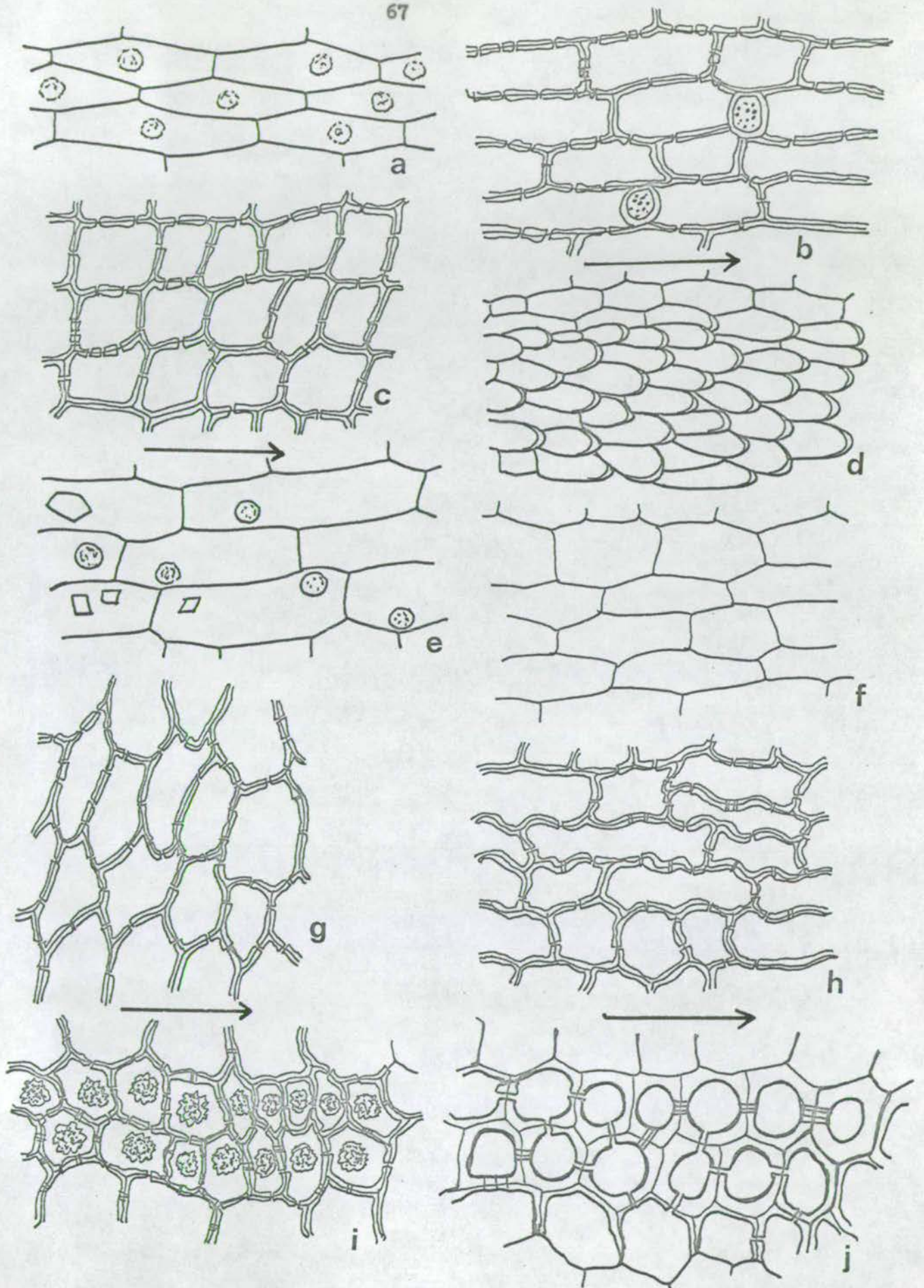
- a. Globba atrosanguinea.
- b. Elettaria surculosa.
- c. Aframomum humburgii.
- d. Roscoea alpina.
- e. Zingiber officinale.
- f. Hornstedtia villosa.
- g. Renealmia bracteosa
- h. Elettaria surculsa
- i. Amomum cardamomum.
- j. Cautleya robusta.

All figures x 680

The arrows show the direction of the longitudinal axis of the lamina.

Fig.11

67



because both are to be found mixed together along the same vein; although there are some species, such as Cautleya robusta (fig. 11.j) and Amomum cardamomum (fig. 11.i), where the costal cells are almost exclusively square in shape.

(ii) The costal cells may be rectangular and/or square as in (i) above, but some of the cells may be isodiametric and with circular thickenings to the inner walls (fig. 11.j) ^{Plate 4.A} / This type is rather of restricted occurrence as it has been seen for Cautleya robusta, C. spicata, C. gracilis, Rhynchanthus longiflorus, Alpinia rufa and A. pahangensis.

(iii) Transversely stretched costal cells. These cells have wider widths than lengths and they become elongated transversely, i.e. perpendicular to the long axis of the veins (fig. 11.g). In surface view, they are usually hexagonal and in some extreme cases they may be less distinguishable from the intercostal cells. This type of cells is more or less characteristic of Renealmia and have been observed in Amomum sp. (B 5303), A. sp. (B 5272), A. sp. (B 2477), A. sp. (B 4756), Alpinia subverticillata, A. oxymitra, A. formosana, A. bracteata, A. elegans, Zingiber gracile, Z. kunstleri, Z. incomptum, Z. sp. (B 4875). Sometimes, the transversely stretched cells may be mixed together with rectangular and/or square cells on the same vein as in Renealmia cabraei and Amomum cardamomum (fig. 11.i).

The walls of the costal cells are usually straight except in few genera where they may be almost sinuous as in Elettaria (fig. 11.h), Hornstedtia, Amomum repoense, A. pierreanum, A. ovoideum, A. speciosa and Languas japonica.

The walls may be thin as in Zingiber and Hedychium, or thick and pitted as in Hornstedtia, Elettaria and Renealmia.

The abaxial intercostal cells are usually much variable and irregular in

shape and size than the adaxial cells. About three arrangements of the abaxial epidermis have been observed in this study. These are:

- (i) Transversely stretched cells. These cells are hexagonal, transversely stretched and perpendicular to the veins. They are usually many times wider than their longitudinal axis. This type of epidermis is common in the tribe Alpinieae, e.g. Elettaria surculosa (fig. 12.a). The epidermis of the tribe Globbeae, some genera of the Hedychieae, e.g. Curcuma, Hedychium and Roscoea, and Zingiber (Zingibereae), is similar to the type described above, but the cells are usually less strongly transversely stretched. They are hexagonal and may be mixed together with rectangular and isodiametric cells. Examples are found in Zingiber officinale (fig. 12.b) and Globba atrosanguinea (fig. 12.d)
- (ii) The cells may be more or less isodiametric in surface view, or a greater percentage of this type may be mixed with some rectangular and hexagonal cells. This is commonly observed in Boesenbergia (fig. 12.c), Kaempferia, Camptandra, Mantisia wardii and Globba winitii.

The epidermis of Scaphochlamys is unique, because the entire abaxial epidermis is uniform, i.e. there is little or no modification of the epidermal cells above the veins (fig. 12.f) except in S. kunstleri and S. tenuis. Also, the epidermal cells are irregular, hexagonal and orientated in different directions.

- (iii) Longitudinal cells. These cells are rectangular, many times longer than broad, and are orientated longitudinally and parallel to the veins. The walls are straight although they may arch over the stomata. This type of cell resembles those of Marantaceae and Strelitziaceae, (see Tomlinson 1969). They have been observed in the following species: Boesenbergia sp. (Woods 1562), (fig. 12.e), B. sp. (Woods 1732), B. sp. (Woods 1549), B. sp. (Woods 1574),

FIG. 12. TYPES OF INTERCOSTAL CELLS

Explanation in the text.

- a. Elettaria surculosa.
- b. Zingiber officinale.
- c. Boesenbergia hutchinsonii.
- d. Globba atrosanguinea.
- e. Boesenbergia ? (Woods 1562).
- f. Scaphochlamys perakensis

The arrows show the direction of the longitudinal axis of the lamina.

All figures x c.180

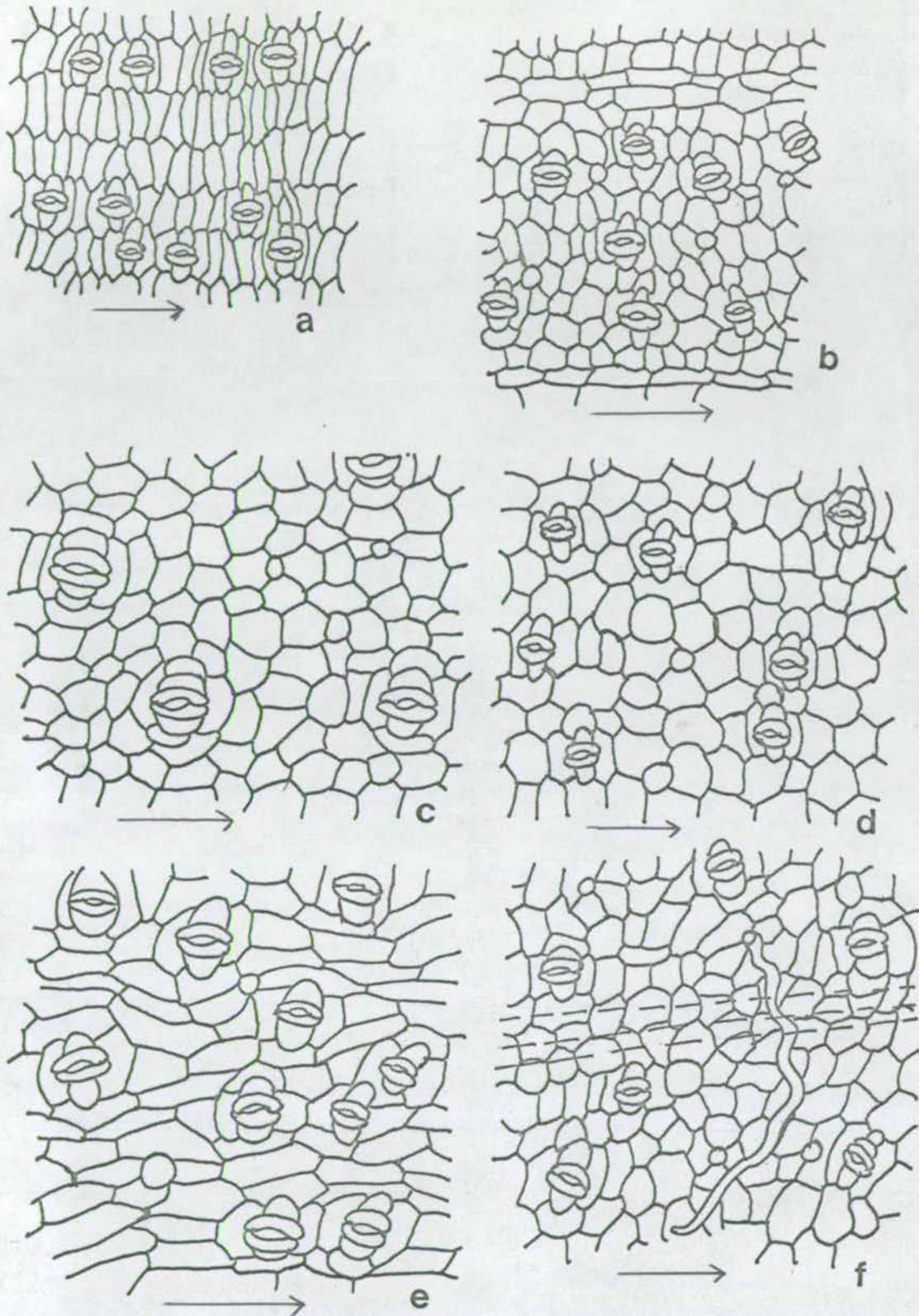


Fig.12

PLATE 4. COSTAL CELLS, STEGMATA, HYPODERMAL FIBRES
AND T.S. LAMINA.

Explanation in the text.

- A. Cautleya robusta (x c.730)
- B. Kaempferia aethiopica (= Cienkowskya
aethiopica) (x c.600)
- C. Aframomum humburgii (x c.300)
- D. Kaempferia pulchra (x c.120)

hy.f.= hypodermal fibres.

si.= silica bodies.

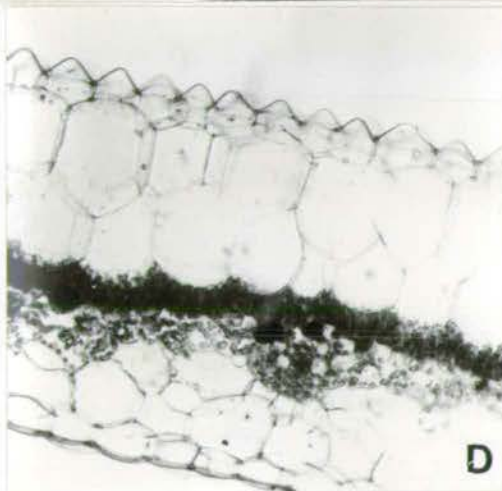
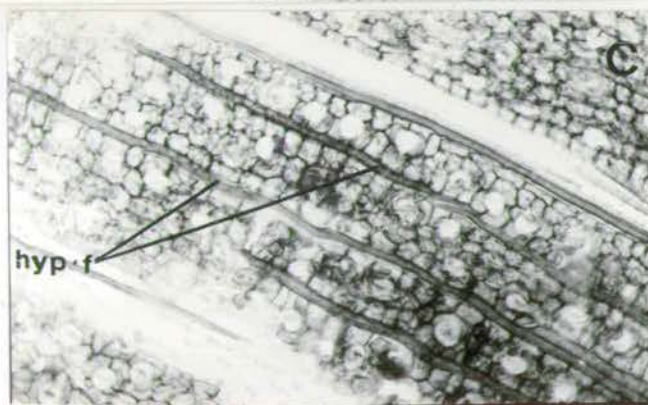
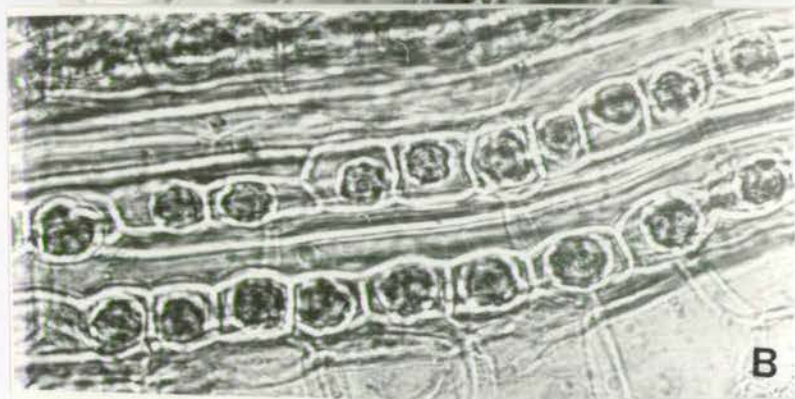
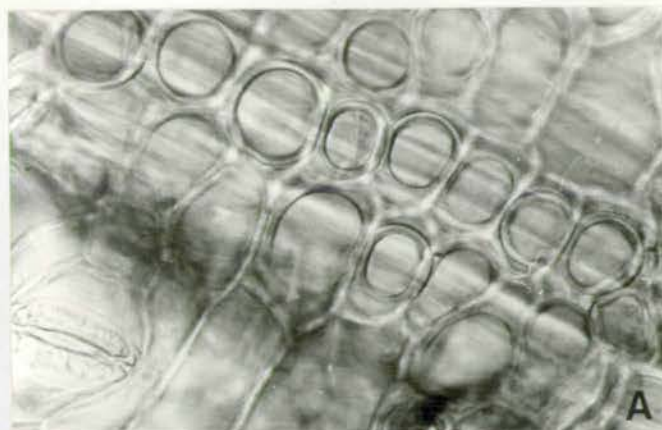


Plate 4

B. sp. (cultivated under the code M. Black 67/1337). The intercostal cells of Alpinia sp. (B 1792) are similar to these cells but they are shorter in length than those in the species of Boesenbergia described above.

It is very interesting to note that all the species mentioned above were collected from the territory of New Guinea. Although they have not been identified to genus or species level because none of them has flowered. Whenever they can be identified, it is probable that they will form a distinct group of species within the genus, or may probably belong to a new genus.

The adaxial cells are more regular () than those on the abaxial epidermis. They are either rectangular or hexagonal and are usually transversely stretched. They vary in size in the different species and their walls are thin to moderately thickened with simple pits. The differences in their relative width and length may be useful as specific character.

INDUMENTUM.

The hairs in the Zingiberaceae have been well studied by Staudermann (1924), Solereder and Meyer (1930), and recently by Tomlinson (1956, 1969). The latter author described the different types and the general distribution of these hairs on the plants.

The hairs are unicellular, and there is considerable uniformity in their structure and shape, except in some genera where there are some structural variations, and on account of these variations, unicellular hairs in the family may be grouped into two categories, viz. (a) simple hairs and (b) branched/stellate hairs.

(a) Simple hairs (fig. 13.a-c; Plate 6.A-C)

The simple hairs are bristles (fig. 13.a,b; Plate 6.A,B), prickles (fig. 13.e,f), delicate hairs (fig. 13.c) or wavy and velvety hairs (fig. 13.g).

The characteristics of the first three types have been described by Tomlinson (1956) and there is no need to repeat them here. However, I will describe the new forms of bristles that have been observed in this study.

(1) The bristles are by far the commonest type of hair in the family. They are similar in structure and are of very limited taxonomic value because of their uniformity and common occurrence. Moreover, they vary much in size and wall thickness, not only on different organs of the same plant, but even on the same lamina. However, the comparative distribution on similar organs of the different species, e.g. ligule, lamina, and inflorescence axis, may be useful along with other characters, for specific separation within a genus.

A very interesting form of bristles, the inflated bristle (fig. 13.b; Plate 6.A), was observed on the sheath of Hitchenia careyana. These inflated bristles have the basal part swollen to many times the width of the shaft. The thickened base of the hair is partially sunken in the epidermis and the distal part of the shaft, above the inflation, tapers to the apex. The walls are thickened and unlignified. These inflated bristles occur along with other normal bristles on the sheath. The physiological reason for the inflation of the bristles is not understood. Similar bristles, although with very short and small inflated base, were found in Zingiber cylindricum. In the genus Hitchenia, it appears that this form of bristle is unique to H. careyana alone. The genus is composed of three species, as was recognised by Schumann (1904), and these bristles were not observed for H. glauca; the third species, H. caulina, was not available for study. However, the presence of the inflated bristles on H. careyana may be useful for separating materials belonging to this species from the others in the genus.

The vegetative parts of most species of Roscoea may appear glabrous,

but it has been observed that papillae-like hairs may be present on the margins of the leaves and floral bracts, particularly near the apices of these organs as in R. alpina (fig. 13.d). Moreover, normal bristles may be present on the lamina of some of the species, as in R. cautleoides.

Velvety hairs are a form of bristles which are usually filiform and may be wavy. Their walls may be thick or thin. Such hairs usually form a velvety felt on the abaxial surface of the lamina in some species as in Cenolophon sp. (B 4989) and Zingiber sp. (Lace 5245). Similar velvety hairs have been observed on the sheath, petiole and ligule of a number of species of Hornstedtia. In these species, the velvety hairs appear as bunches or patches which are more or less adpressed to the surface of the sheath (fig. 13.g). These hairs, together with the usually raised transverse veinlets in these species, give a characteristic pattern to the surface of the sheath, ligule and sometimes floral bracts in Hornstedtia. The presence of velvety hairs is almost a generic character for Hornstedtia, but are not present in all the species and they occur sporadically in a few species of other different genera, such as in Alpinia, Amomum and Cenolophon.

(ii) Prickles are of a rather limited distribution and they may be of taxonomic value in the taxa where they occur. Tomlinson (1956) reported them in one species of Aframomum out of about fifty species in the genus, and also in Alpinia javanica, Cautleya spicata and Hornstedtia conica. In this study, prickles have been observed, along with bristles, in two species of Aframomum, one Cenolophon and Riedelia sp. (fig. 13.e).

Another very interesting form of prickles are the prickle-like sclereids (fig. 13.f-1) observed on the sheath and petiole of Hornstedtia leonurus. These structures are different from the prickles described by earlier workers.

They are sub-epidermal in their position and they may, probably, be of sub-epidermal origin. Their walls are well thickened, pitted, laminated and lignified. Most of these 'prickles' bear sharp or blunt and short projections to and beyond the epidermis. Towards the margins of the sheath (fig. 13.h) some of these prickles become more stout and some point inwards instead of outwards. In surface view (fig. 13.i), they appear as 'papillae' on the surface of the epidermis and their walls appear to be continuous with those of the surrounding epidermal cells. When some of the projections are displaced, their cavities appear uniform round their edges without any sign of rupturing in the epidermis. In the hypodermal position these prickles are surrounded by other sclereids which are without projections to the outside, although occasionally some have their sharp points orientate^d/towards the epidermis. Normal bristles are also present on the sheath and these have their bases in the epidermis. These prickles and sclereids together form a rigid mechanical zone on the abaxial sub-epidermal layers of the sheath and petiole of H. leonurus (fig. 9.g; 13.f,h; Plate 6.B,C).

Although living specimens of this species were not available for the study of the development, the recent publication on the development of stinging hairs in Dalechampia roezliana (Euphorbiaceae) by Thurston and Lersten (1970) threw some light on the problem. They suggested that the ontogeny of stinging hairs of D. roezliana, as was described by Knoll (1905) were similar to that of Tragia, another genus in the Euphorbiaceae. According to these authors, "the central cell is initiated in the sub-epidermal layer and intrudes among the epidermal cells". It is most probable that the prickles observed in H. leonurus arose from the sub-epidermal position and extrude among the epidermal cells. But the authors mentioned above did not explain whether, due

FIG. 13. TYPES OF SIMPLE HAIRS.

Explanation in the text.

- a. Globba atrosanguinea.
- b. Hitchenia careyana.
- c. Zingiber officinale.
- d. Roscoeia purpurea.
- e. Cenolophon sp. (B 5166).
- f. Hornstedtia leonurus.
- g. H. reticulata.
- h. H. leonurus.
- i. H. leonurus.

Figures a - f, h, i. x c.680)
figure g. x 5;

pr. scl.= prickle-like sclereids.

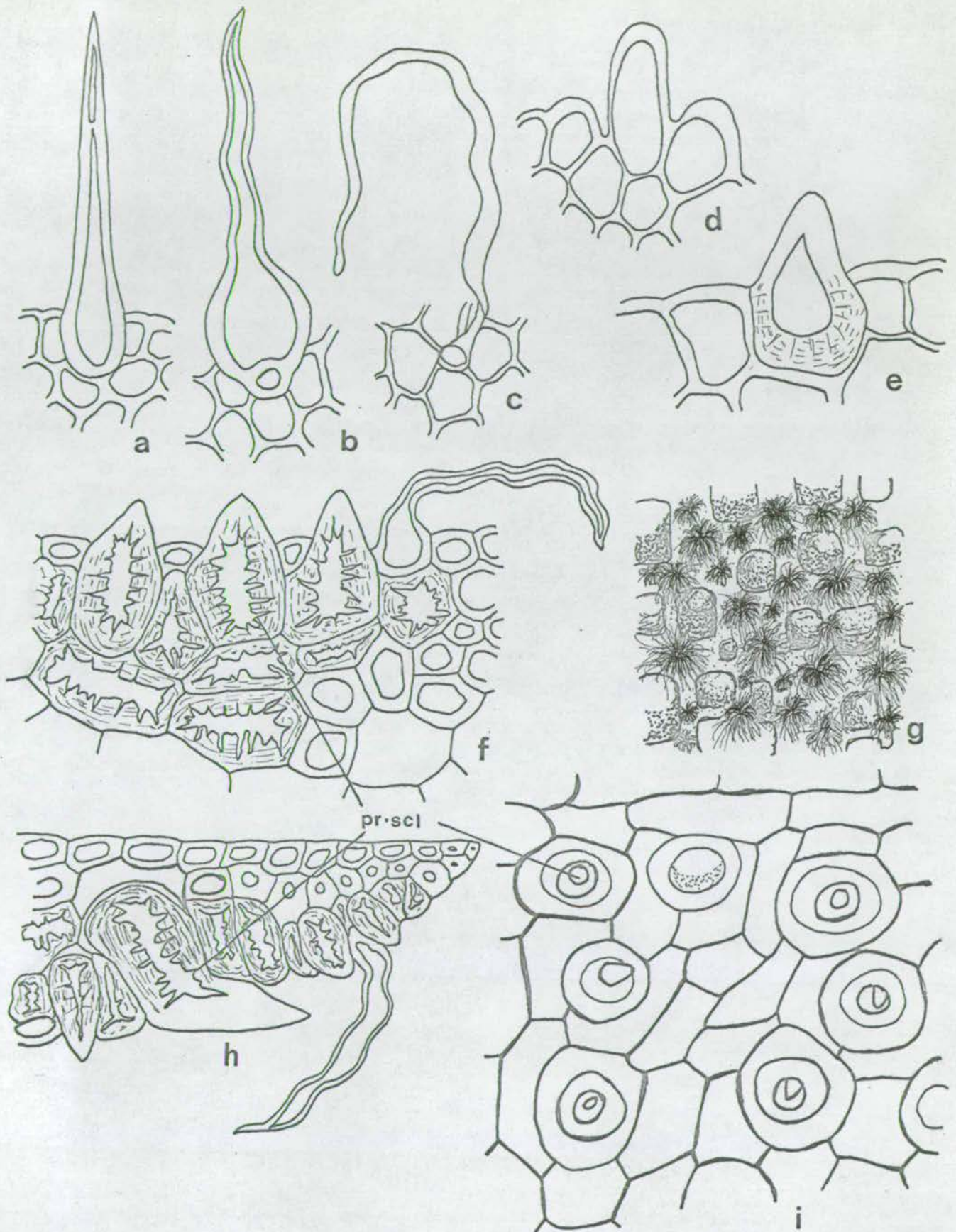


Fig.13

to such intrussive growth, the originally intact epidermis was broken or not, and whether there was any sign of such rupture in the epidermis. In this species, it is difficult to observe any rupturing in the epidermis even if it is present, because the intrusive growth must have taken place very early in the ontogeny of the sheath, the cellular alignment must have been smoothed out during the stages of establishments and maturation of all the cells together. But the fact that the projections on these prickles are easily removable from the epidermis and without any damage to the adjacent cells, may support the fact that these prickle-like sclereids are not epidermal but sub-epidermal in origin.

H. leonurus is an anomalous species among the others in the genus Hornstedtia, and the presence of the prickle-like sclereids probably confirms its uniqueness in the genus.

(iii) The delicate hairs (fig. 13.c) are found on, and characteristic of the following genera; Scaphochlamys, Kaempferia (including Haplochorema uniflorum), Boesenbergia, Camptandra, Caulokaempferia, all in the tribe Hedychieae, and Zingiber (Zingibereae). The former six genera could easily be separated from all others in the family by the presence of these characteristic delicate hairs.

(b) Branched/stellate hairs (fig. 14.a-n; Plate 5.)

Branched/stellate hairs were first reported for the family by Solereder and Meyer (1930) on some species of Renealmia, including R. exaltata which has also been seen for this study. Recently, Tomlinson (1956) reported this type of hairs on two species of Renealmia and one of Aframomum. Branched/stellate hairs have been observed in the materials for fifteen species of Renealmia, two species of Rhynchanthus and one of Riedelia. The fifteen

species of Renealmia were those available out of about fifty-seven species recognised in the genus by Schumann (1904). But it may be interesting to note that these fifteen species examined were distributed in the two series and sub-series of the genus (Schumann 1904) and furthermore, they include species from both South America and Africa. This seems to be an approximate cross-section of the major divisions within the genus as well as a fair representation from all over the range of distribution of the genus.

The branched/stellate hairs are so called because, in the species where they have been observed, the number of branches varies much, even on the same lamina. These may be two or more and hairs with many branches which are disposed + radially round a central pore occur frequently alongside those with two to three branches (Plate 5.A,B). Most of these hairs are dichotomously branched as in Renealmia antillarum (fig. 14.a; Plate 5.E). They are usually stalked and their bases are sunken in the epidermis. In some species, e.g. R. bracteosa (Plate 5.D), the stalk (base) is short and the hairs may appear sessile. The bases are usually as thick as the shaft or may be thicker and sclerized as in R. occidentalis (fig. 14.b; Plate 5.C). The walls are fairly thickened in some hairs so that the branches may become solid towards the apices (fig. 14.c.d). The walls are not lignified but are composed of cellulose with a thin layer of cuticle to the outside. The lumen in most of these hairs contain tanniniferous substances which usually appear dark brown to golden yellow in the unstained specimens. One other characteristic of these hairs is that most of them are perforated in the centre with a more or less circular pore as seen in surface view (fig. 14.a-n; Plate 5.A,B,F). Normal type of bristles also occur together on the same organ as the stellate hairs in some species.

FIG. 14. TYPES OF BRANCHED/STELLATE HAIRS.

Explanation in the text.

- a. Renealmia antillarum.
- b. - c. R. occidentalis.
- d. - f. R. exaltata.
- g. - h. R. spicata.
- i. - j. Rhynchanthus longiflorus.
- k., l. R. beesianus.
- m., n. Riedelia sp. (Millar 14594).

All figures x c.680.

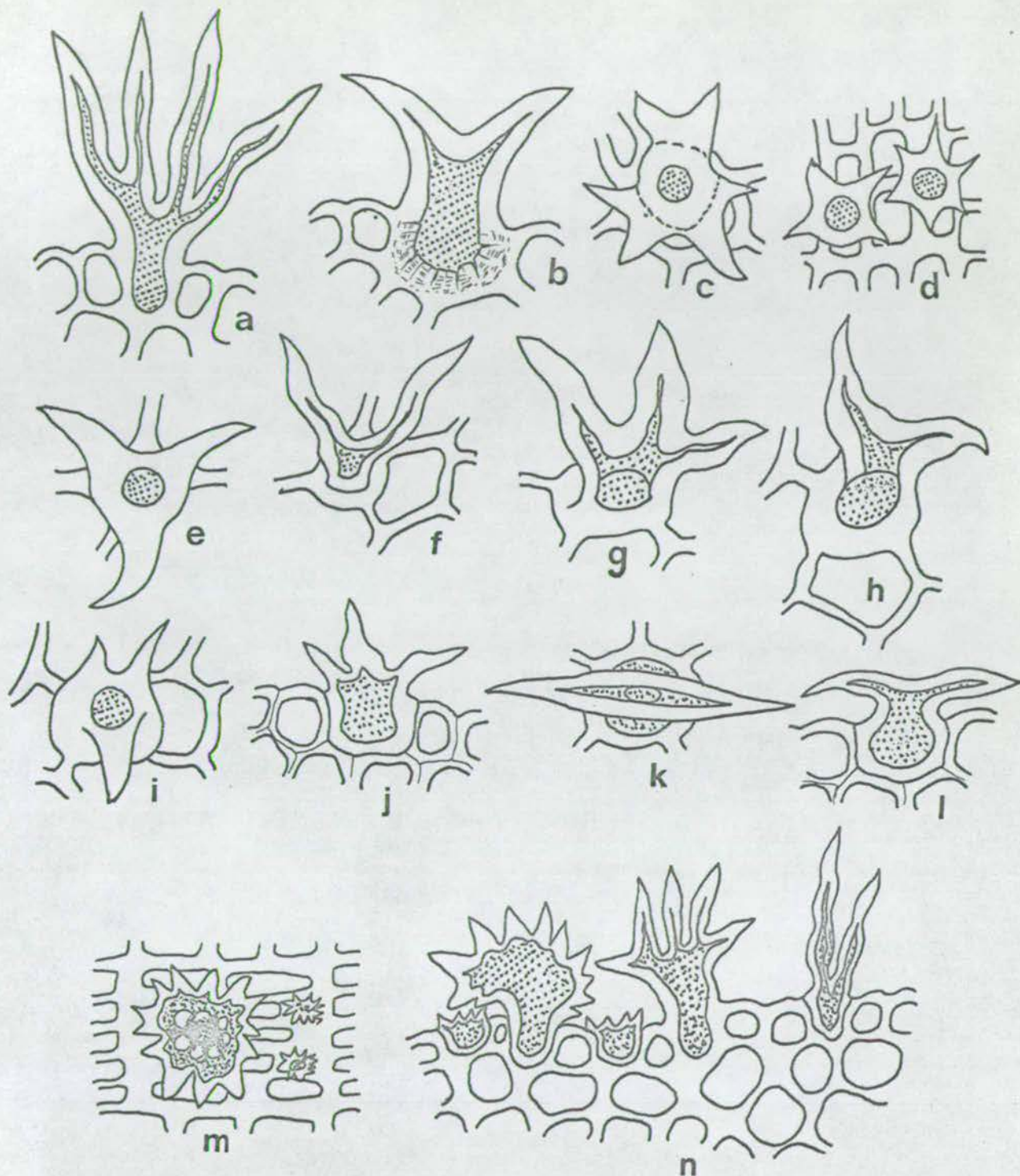


Fig. 14

PLATE 5. BRANCHED/STELLATE HAIRS.

Explanation in the text.

- A. Renealmia exaltata (x c.340)
- B. R. exaltata (x c.545)
- C. R. occidentalis (x c.475)
- D. Riedelia sp. (Miller 14594) (x c.700)
- E. Renealmia
A. anillarum (x c.465)
- F. Riedelia sp. (Miller 14594) (x c.650)
- G. R. sp. (Miller 14594) (x c.650)

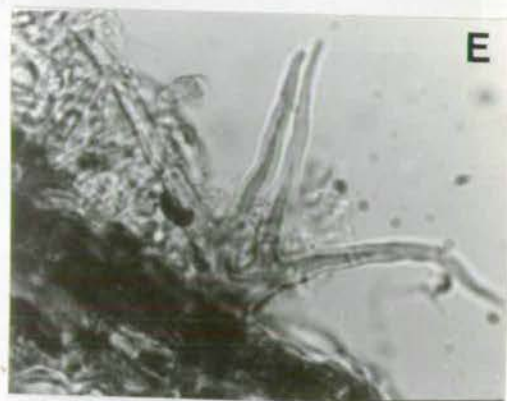
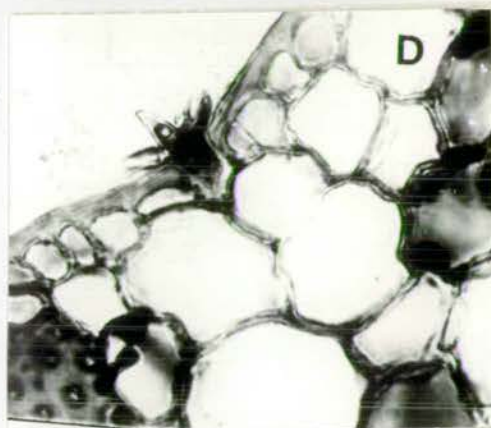
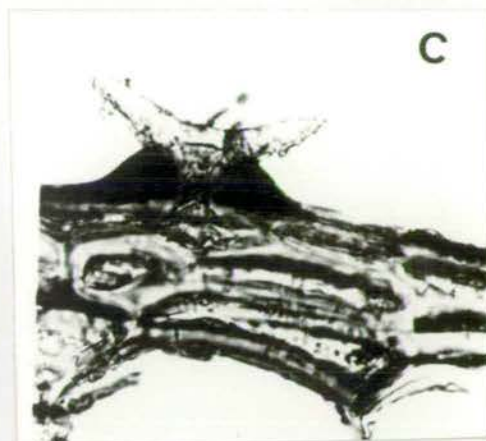
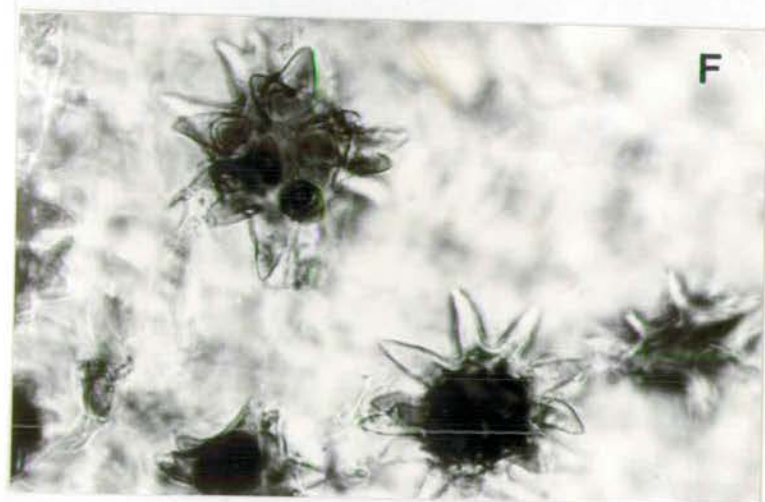
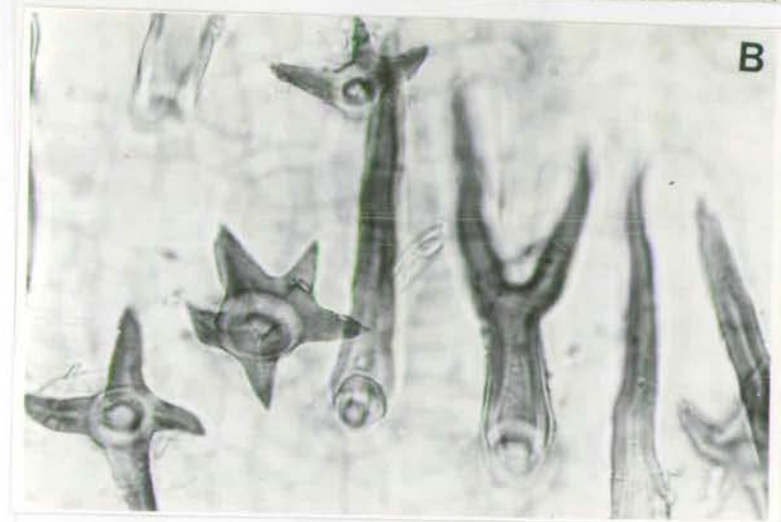


PLATE 6. SIMPLE HAIRS.

Explanation in the text.

A. Hichenia careyana (x c.750)

B,C. Hornstedtia leonurus (x c.700)

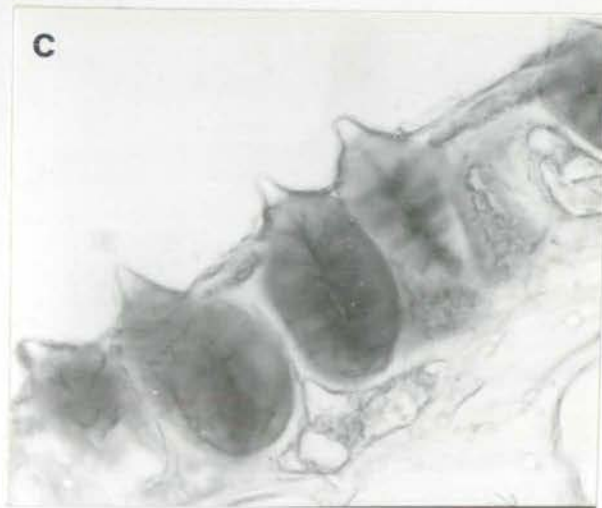


Plate 6

There are some differences observed in the structure, size and distribution of these hairs among the species of the three genera Renealmia, Rhynchanthus and Riedelia. Within the genus Renealmia, the hairs are different in size and shape in the different species. For instance, the branches are usually long and more slender in R. antillarum (fig. 14.a; Plate 5.E) than in R. occidentalis where they are shorter but more stout. The density of the hairs varies on the different organs of the same plant, but the comparative density on similar organs might be useful for separating two closely similar species. The ligule of R. exaltata (Plate 5.A) is probably the densest observed out of all the species in the genus.

The commonest hairs on the sheath of Riedelia sp. (Millar 14594) are more or less truly stellate because they have many branches which are radiate on the apex (fig. 14.m,n; Plate 5.F,G). Apart from these large stellate hairs, there are several minute, sessile stellate hairs whose branches just manage to project above the epidermis. These hairs are similar in size to the adjacent epidermal cells (fig. 14.m,n) and it seems that the whole epidermis of the sheath contains hairs. The structure of these hairs is unique to Riedelia spp., as such has neither been observed on any other species nor reported anywhere in the literature.

The hairs of Renealmia and Rhynchanthus are similar in structure although there may be some useful specific differences between the species. It is noteworthy that in the family branched/stellate hairs are rare but have been observed in eighteen species belonging to the three genera mentioned above. These hairs are probably diagnostic for Renealmia and this need to be confirmed when further investigation is made on the remaining species of the genus which were not available for this study.

LAMINA ANATOMY.

MIDRIB.

For comparative purposes, the anatomy of the lamina was studied from the transverse sections taken at the standard level midway between the base and apex. There are differences between different species in the anatomy of the midrib, and these differences depend on the level of divergence of the vascular bundles from the midrib into the lamina. In those genera where most of the midrib vascular bundles diverge into the lamina above the base and before the standard median level, few vascular bundles from one to three, and occasionally only one, may be found in the midrib. In such cases, the midrib is not usually prominently raised above the lamina. Examples are found in Kaempferia (fig. 15.a), Camptandra, Boesenbergia and Scaphochlamys. Where the vascular bundles diverge gradually and at an almost regular interval, there are usually many more than three vascular bundles within the midrib at the standard level. Examples are found in Globba (fig. 15.b), Hedychium (fig. 15.c) and most genera in the tribe Alpinieae, e.g. Hornstedtia pininga (fig. 15.d).

As in the sheath and petiole, the vascular bundles of the midrib have been grouped into similar systems of arcs from I-IV. The differences in the midrib between species are found in the number of the arcs present as well as the variation in the ground and mechanical tissues. Arc I vascular bundles (fig. 15.c) are always present in all species, although the number varies from species to species. In Kaempferia, Boesenbergia, Scaphochlamys and Camptandra, the number varies between one and three (fig. 15.a), whereas in

Alpinieae arc I vascular bundles are usually many and congested (fig. 15.d).

Arc II vascular bundles are present in the abaxial position in the following genera and species: Globba (fig. 15.b), Hedyohium (fig. 15.c), Brachyichilum, Scaphochlamys, Boesenbergia (except for a few species such as B. hutchinsonii and B. sp. (B & M 5164), Kaempferia aethiopica (= Cienkowskya aethiopica), Alpinia calcarata, A. pulchra, A. allughas, Catimbium speciosa. The arc II may be present and pectinate with vascular bundles of the main arc I as in Roscoeia (fig. 15.e), Renealmia exaltata, R. antillarum, Cantleya spicata, Alpinia subverticillata, A. sp. (Score 2316) and A. allughas. The arc II vascular bundles are usually absent from the midrib of most genera of the Alpinieae (fig. 16.a-g), except those mentioned above.

Although the arc IV system is usually less developed or absent in the midrib, it has been observed in a number of species in some different genera of the Alpinieae. These are Achasma megalochelios (fig. 16.a), A. subterranean, Hornstedtia leonurus (fig. 17.e), Alpinia calcarata, Amomum trilobium, A. hewithii, (fig. 16.d), Catimbium speciosa, Elettaria cardamomum, Phaeomeria venusta, P. speciosa and Riedelia sp. In these species the arc IV bundles are usually smaller than those in the arc II and III systems. They are also fewer in number and are attached very close to the adaxial epidermis. These bundles are identical with the arc IV of the petiole.

MECHANICAL TISSUE.

Mechanical tissue similar to those already described for the sheaths and petioles, have been observed in the midrib of a number of species in the Alpinieae. In the midrib this tissue is produced in a number of ways,

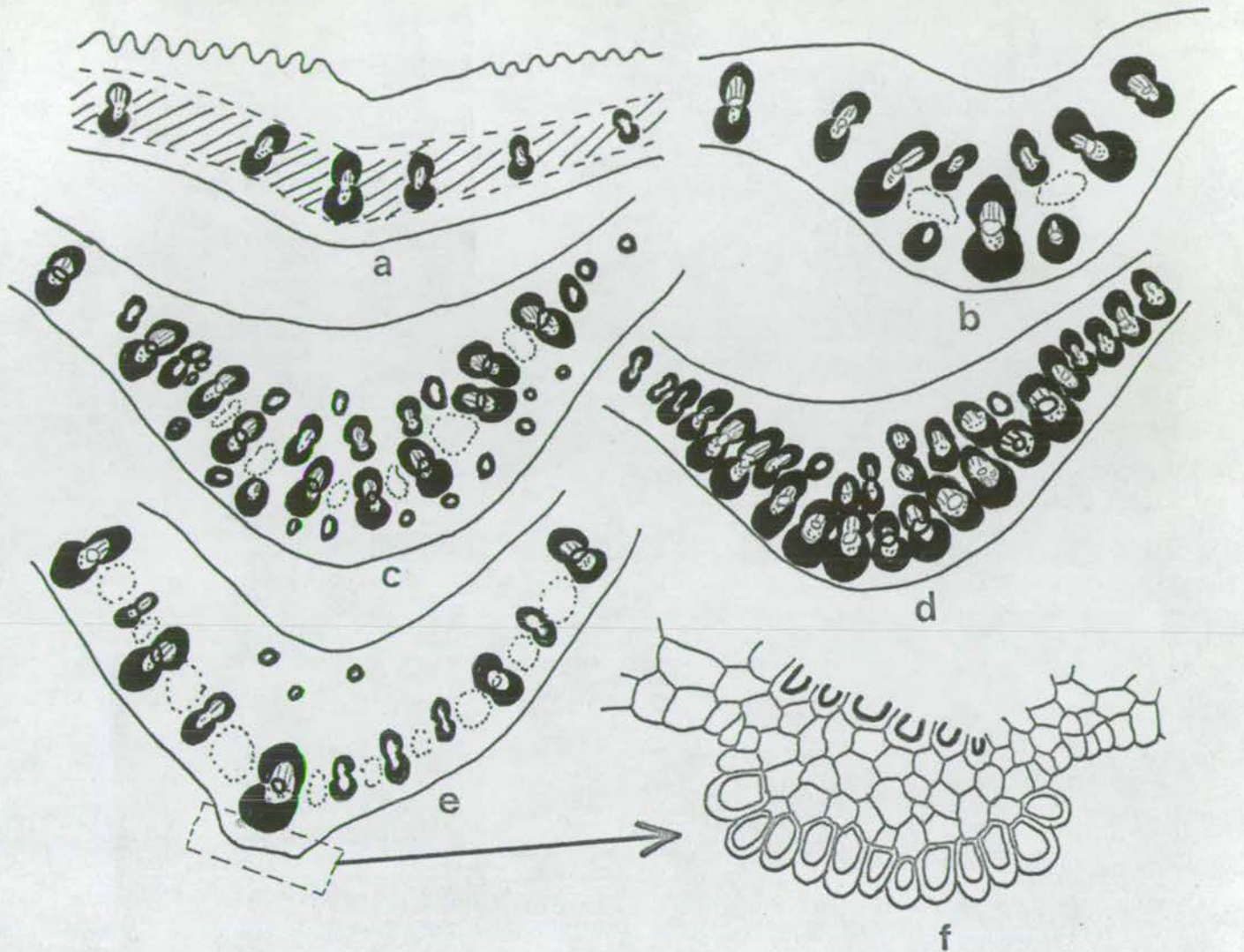


Fig. 15

FIG. 15. TRANSVERSE SECTIONS THROUGH THE MIDRIB.

Explanation in the text.

- | | | |
|-----|--------------------------------------|----------|
| (a) | <u>Kaempferia elegans.</u> | (x 31) |
| (b) | <u>Globba atrosanguinea.</u> | (x 62) |
| (c) | <u>Hedychium thyrsiforme.</u> | (x 31) |
| (d) | <u>Hornstedtia pilinga.</u> | (x 31) |
| (e) | <u>Roscoea alpina.</u> | (x 31) |
| (f) | <u>R. alpina.</u> - detail of 'Keel' | (x 180). |

viz:- (i) By the extension of the bundle sheath of the main arc I vascular bundles. These bundle sheaths extend laterally and coalesce with the adjacent sheaths to form a rigid fibrous zone. This tissue is always close to the abaxial epidermis. Examples are found in Alpinia conchigera (fig. 17.a), A. calcarata, A. galanga, A. rufa, A. allughas (fig. 17.b), Phaeomeria venusta (fig. 17.d), Amomum sp. (B 5334), Aframomum humburgii, Achasma sp. (B 5303), Elettaria surculosa, Renealmia exaltata, and R. antillarum.

(ii) There may be gaps between the extended bundle sheaths and these may be bridged by sclereids or sclerized cells as in Alpinia pulchra (fig. 17.c), A. subverticillata, A. sp. (Corner 106, 107), A. sp. (Score 2316) and Hornstedtia leonurus (fig. 17.e). (iii) Apart from the abaxial mechanical tissue described below, adaxial fibrous or sclerotic tissue may be present in some species. This tissue may be produced by moderately thick-walled sclerenchymatous cells as in Phaeomeria magnifica (fig. 16.f), or thick-walled sclerenchymatous cells as in Alpinia pulchra (fig. 17.c), A. subverticillata, A. allughas, A. formosana, A. sandarac, A. intermedia, A. sp. (Corner 106, 107), A. sp. (Score 2316), Elettaria surculosa, E. cardamomum, Hornstedtia leonurus, Catimbium speciosa, Cenolophon oxymitrum, and Achasma megalocheilos.

(iv) The median adaxial fibrous tissue may be flanked on either side by few small vascular bundles as in Achasma megalocheilos (fig. 16.a). This arrangement is almost diagnostic for the genus Achasma. (v) In the midribs of Alpinia allughas (fig. 17.b), Catimbium speciosa, Cenolophon oxymitrum (fig. 17.f,g), there are isolated fibrous strands which appear as a continuation of the hypodermal fibres observed in the lamina. These strands appear similar to those described above, except that the median sclerenchymatous, rigid zone is lacking. Although, where these strands are close together, they may produce similar strengthening tissue. The fibrous strands in the midrib of

FIG. 16. EXPANSION CELLS.

Explanation in the text.

- a. Achasma megalocheilos (x 31)
- b. A. megalocheilos - detail of expansion
cells (x 680)
- c. Alpinia sp. (B 4876) (x 15)
- d. Amomum hewithii (x 62)
- e. Alpinia intermedia (x 31)
- f. Phaeomeria magnifica (x 62)
- g. Elettaria sp.

exp.c = expansion cells;
sc.t = sclerotic tissue.

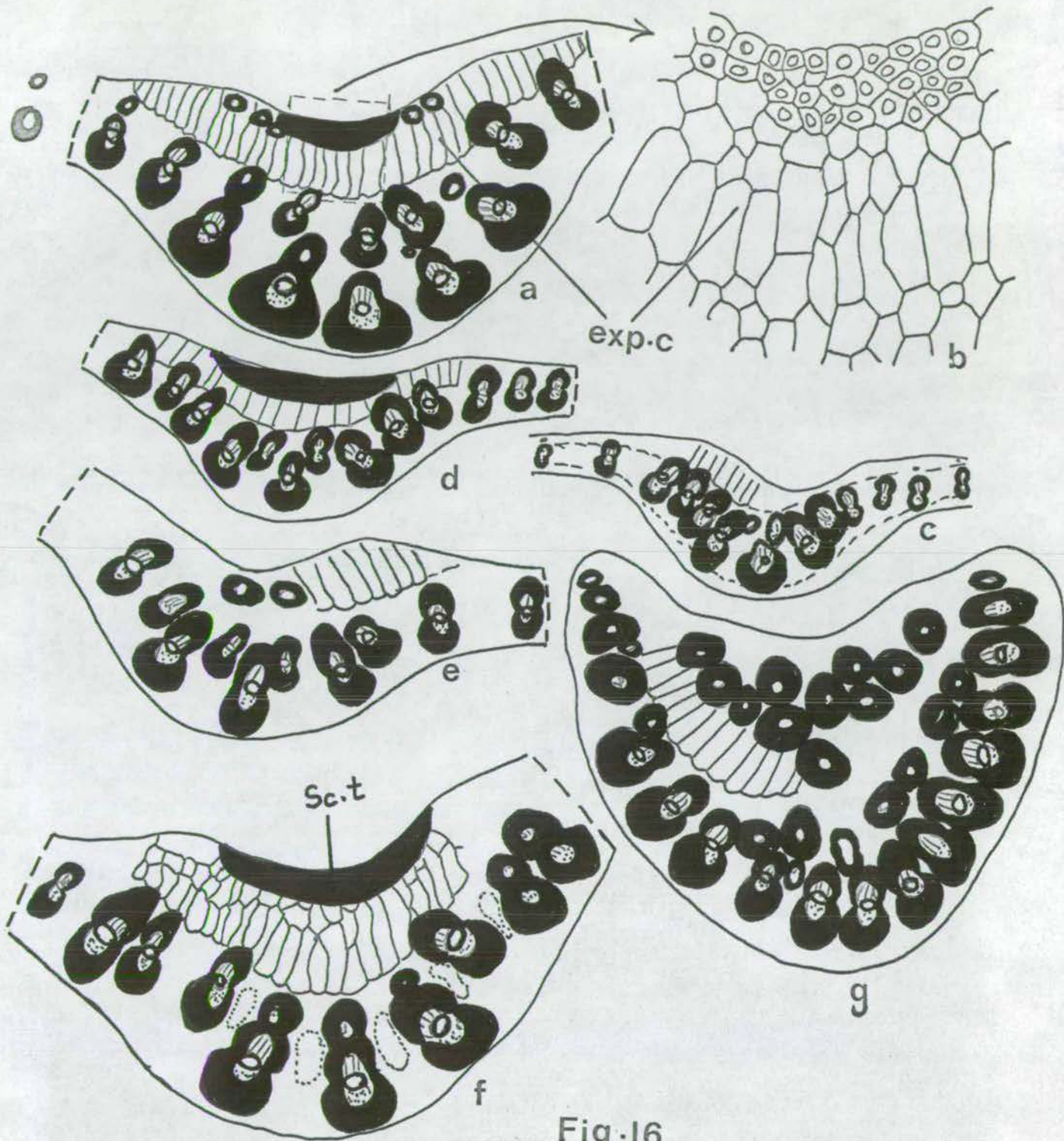


Fig. 16

FIG. 17. TRANSVERSE SECTIONS THROUGH THE MIDRIB
OF LAMINA SHOWING MECHANICAL TISSUE.

Explanation in the text.

- a. Alpinia conchigera (x 62)
- b. A. allughas (x 31)
- c. A. pulchra (x 31)
- d. Phasomeria venusta (x 31)
- e. Hornstedtia leonurus (x 31)
- f. Catimbum speciosa (x 31)
- g. Cenolophon oxymitrum (x 31)

Scl. = Sclereids; Scl. = Sclerotic tissue;
m.t = mechanical tissue.

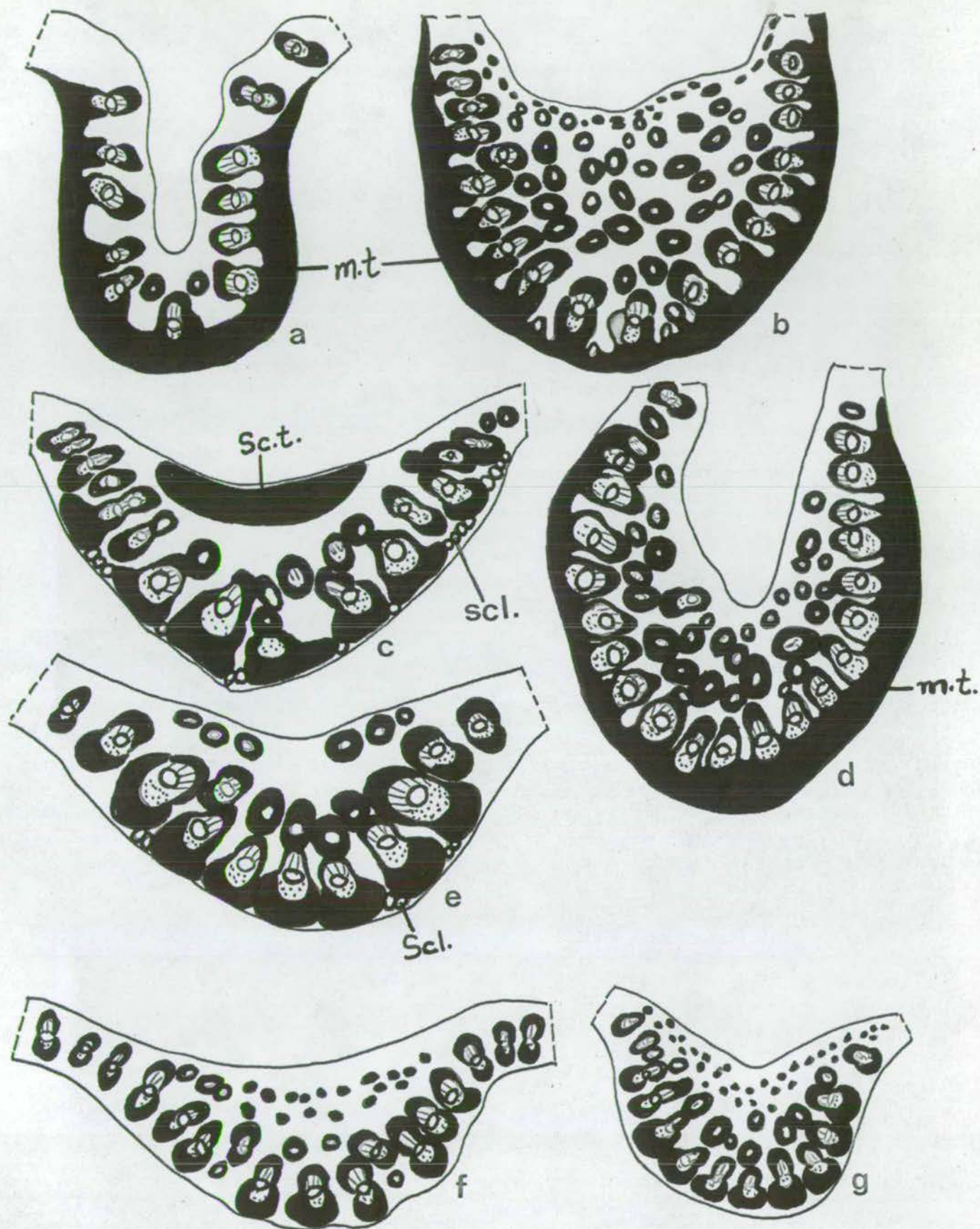


Fig. 17

Hornstedtia leonurus (fig. 17.e) is similar to some species of Achasma in this respect.

SCLEROTIC PHLOEM ELEMENTS (fig. 18).

Phloem fibres are common in the dicotyledons but sclerotic phloem is not widely reported for the monocotyledons. Examples of the sclerotic phloem are to be found in the Gramineae, particularly in the following species, Cortaderia selloana and Desmostachya bipinnata. These were reported by Metcalfe (1960).

The first information concerning the possible sclerification of the phloem elements in any member of the Zingiberaceae was that reported for Hornstedtia pinginga (then known as Donacodes pinginga), by Solereder and Meyer (1930).

Recently, Tomlinson (1956, 1969) reported the presence of sclerotic phloem parenchyma cells in Hornstedtia scyphifera and H. conica. This tissue has been observed in all the sixteen species of Hornstedtia, including H. pinginga and H. scyphifera, except H. leonurus, out of about sixty species known in the genus. Fig. 18 shows the extent of the sclerification in the phloem of H. scyphifera. These sclerotic cells were also observed in Amomum sp. (B 5159 aff. Xanthophegium), Alpinia intermedia and Zingiber sp. (B 4875 - epiphytic species). The sclerotic cells are thick-walled and lignified. They are usually irregularly arranged and this probably supports the suggestion by Tomlinson that it might be the phloem parenchyma cells that become sclerotic. Although less than half of the known species of Hornstedtia has been seen, the comparison of these observations with those of earlier workers suggests that the sclerotic phloem cells might be diagnostic for the

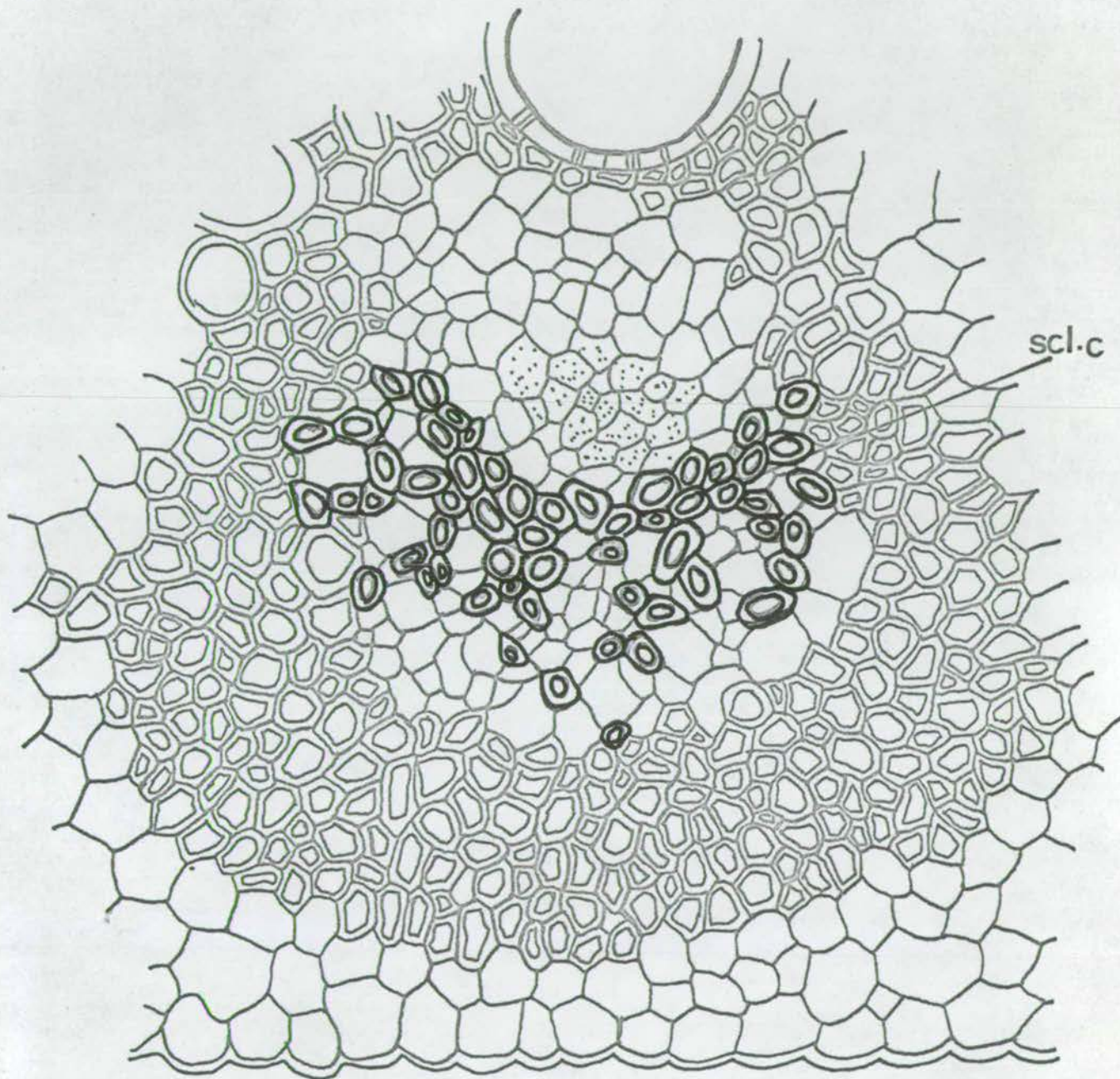


FIG. 18

FIG. 18. SCLEROTIC PHLOEM ELEMENTS IN HORNSTEDTIA.

Details of part of the Vascular bundle
and sheath. (x c. 680)

scl. c. = Sclerotic cells.

genus Hornstedtia, except Hornstedtia leomurus. Further investigation on the remaining species in the genus, which were not available for this study, is much needed to confirm this.

"EXPANSION CELLS" (fig. 16.a-h).

Certain cells towards the adaxial side of the ground tissue of the petiole and midrib may become greatly elongated and enlarged more than the rest of the surrounding cells. These cells have been referred to as expansion cells (Tomlinson 1956, 1969). Expansion cells are almost a constant characteristic of the lamina in the following families of the Zingiberales, viz:- Musaceae, Heliconiaceae, Strelitziaceae, some species of Zingiberaceae, Marantaceae, but not in Lowiaceae and Costaceae. Each of the six families, where expansion cells are reported, differs from one another in the position and type of these cells (see Tomlinson 1969).

In the Zingiberaceae, cells similar to expansion cells are also found in the petiole and midrib of the lamina, and rarely in the sheath except in Boesenbergia sp. (B & M 5164) discussed on page 62. Expansion cells vary in the position in which they are found in both the petiole and midrib. They may occupy the median position as in the midrib of Achasma megalochelios (fig. 16.a,b), and Amomum hewithii (fig. 16.d), Phaeomeria magnifica A. sp. (B 5279). These cells could be found towards both or either side of the midrib and petiole as in Alpinia sp. (fig. 16.c), A. blepharocalyx, A. intermedia (fig. 16.e), Elettaria sp. (B 2577) (fig. 16.g), and Plagiostachys sp. (B 5429).

The function of the expansion cells is not clear, although that of rolling and unrolling the leaf was suggested for them (Tomlinson 1956). It seems

that this suggestion might be true for those families where the expansion cells are found in the hypodermis or the epidermis above the veins as in Musaceae, Heliconiaceae and Strelitziaceae. It is difficult to see how these cells perform such a function in the few species of Zingiberaceae where they are found within the petiole and midrib of the lamina. It could be that they remain as one of the 'relict' characters in this family and that they take part in fluid exchanges by storing water and/or gases.

EPIDERMIS (in transverse section).

The cuticle protecting the epidermis is very thin except in Alpinia pulchra where it is thick (fig. 19.d). It is true, as was reported by Tomlinson (1956), that the cuticle may often penetrate into the base of the sub-stomatal chamber. Also the minutely papillate cuticle he reported in Kaempferia gilbertii, K. angustifolia and Hedychium gardnerianum has been observed and confirmed for these species.

There are differences between different species in the shape and size of the epidermal cells. These differences are probably of specific value rather than for generic determination. However, it is worthy of note that the epidermis is narrow in Boesenbergia (fig. 23.a,b), and few species in some other genera, e.g. Aframomum humburgii, Alpinia samoensis (fig. 19.c) and A. sp. (Score 2316).

Papillate epidermis was reported by Tomlinson (1956) for Kaempferia rotunda and Costus malortieanus (Costaceae). In this study, it has been observed in many species of Kaempferia and few in Boesenbergia. The adaxial epidermis is papillate in the following species:- Kaempferia angustifolia (fig. 19.e), K. elegans (fig. 23.d; Plate 4.D), K. rotunda, K. pulchra, K. gilbertii, K. marginata, K. pandurata, K. sp. (B 4775), Boesenbergia sp.

(B & M 5164), B. sp. (B 4900). The abaxial epidermis is slightly papillate in the following species:- Kaempferia elegans (fig. 19.e), K. angustifolia, K. gilbertii, Boesenbergia parvula, B. sp. (B 5146); the abaxial epidermis of Boesenbergia sp. (B. 4927) is different from any of the species of Kaempferia and Boesenbergia. Instead of each epidermal cell being papillate, the epidermis forms multicellular papillae or turrets and the stomata are found on top of each of these turrets (fig. 23.b; & 29.c)

The epidermis of the African Kaempferias (Cienkowskya) is never papillate as in the Asiatic Kaempferias. Papillate epidermis is probably diagnostic for Kaempferia, but the presence of this character in some species of Boesenbergia appears to reduce the diagnostic value.

HYPODERMIS.

The hypodermis is very variable not only from species to species but also at different levels on a lamina. The number of layers of the hypodermis varies from the midrib to the margins. Where there are from one to three layers near the midrib, the hypodermis might be reduced to one layer, or may not be developed near the margin.

The hypodermis is made up of large or small colourless cells which occasionally contain crystals of calcium oxalate, tannins, oil cells or silica bodies as in Kaempferia aethiopica (= Cientowskya aethiopica) (fig. 25.6). The cells vary in size and are usually larger than the epidermal cells except in few cases, e.g. Alpinia samoensis (fig. 19.c) where cells of both layers are almost similar. In transverse section, the shape of the hypodermal cells vary between cubical or isodiametric cells, hexagonal to rectangular and narrow cells (fig. 19.a-e; 23.a-f).

The differences in the hypodermis of the different species may be observed in the same patterns as were discussed by Tomlinson (1956). These are:- the hypodermis may be:

(i) Completely absent from both surfaces as in African Kaempferias, e.g. K. aethiopica, (fig. 23.c), Alpinia parviflora, A. graminacea, A. intermedia, A. javanica, Cyphostigma pedicellatum, Phaeomeria magnifica, Zingiber officinale and plagiostachys except P. paradoxa and P. sp. (B 5525). The absence of the hypodermis in the median level of the lamina of the African Kaempferias is probably another distinguishing character for separating these groups of species from the Asiatic Kaempferias, where the hypodermis is well developed (fig. 19.e; 23.d).

(ii) Present on one surface only, i.e. present on (a) adaxial surface only, e.g. Renealmia bracteosa (fig. 21.A). The observation made on Kaempferia gilbertii, does not agree with Tomlinson's observation on this species. The hypodermis is well developed on both surfaces at least beyond the standard level taken for the observation. (b) on abaxial surface only, e.g. Globba atrosanguinea (fig. 23.e), G. bulbifera, G. schomburgkii, G. winitii, Mantisia wardii, Camptandra and few species in Zingiber, e.g. Z. puberulum, Z. kerrii and Z. mollis. This type of hypodermis is very common or typical of Globba and Camptandra and may be found in few species of other genera in the Alpinieae.

(iii) Present on both surfaces. This is the most common type, examples are: Boesenbergia plicata (fig. 23.a), Kaempferia elegans (fig. 23.d), K. angustifolia, Hedychium, Brachychilum, Roscoeia, Curcuma, Scaphochlamys.

Other differences in the hypodermis such as the relative size of the epidermal cells to the hypodermal cells and the individual size of the latter

are probably of specific importance rather than of generic value.

THE VEINS OF THE LAMINA.

The veins of the lamina are very variable in size and consist of large, medium-sized and small vascular bundles. These bundles are the direct continuation into the lamina of arc I, II and III of the petiole and midrib. The large bundles often contain one or two large metaxylem elements and these may be surrounded by few smaller elements. In the medium-sized and smaller bundles the metaxylem elements are small and vary between one and three. The xylem of the smallest bundles consists of mainly xylem fibres. The phloem is abaxial to the xylem from which it is separated by one to two rows of conjunctive cells. The phloem consists of sieve elements, companion cells and phloem parenchyma.

Like all other vascular bundles in the plant, the vascular bundles of the lamina are usually sheathed by two bundle sheaths. These are the outer and the inner sheath. The former is composed of parenchymatous cells while the latter is made up of sclerenchymatous fibres. According to Tomlinson (1956), there is variation in the degree of differentiation of the bundle sheath in the different species, and also with the size of bundles.

The bundle sheath of the smallest bundles may consist entirely of parenchymatous cells (fig. 20.A), while in the medium-sized bundles, the sheath may consist of sclerenchymatous abaxial cap and parenchymatous adaxial cap. In the large bundles the sheath is usually composed of sclerenchymatous fibres (fig. 20.C,D), which vary in thickness from species to species. It may be separated into adaxial and abaxial caps by large, colourless parenchymatous cells (fig. 20.B,C,D).

In some genera, the bundle sheath may be extended as a fibrous plate, of

FIG. 19. TRANSVERSE SECTIONS THROUGH THE LAMINA.

Explanation in the text.

- a. Alpinia chinensis (x 62)
- b. A. parviflora (x 62)
- c. A. samoensis (x 62)
- d. A. pulchra (x 62)
- e. Kaempferia angustifolia (x 180)

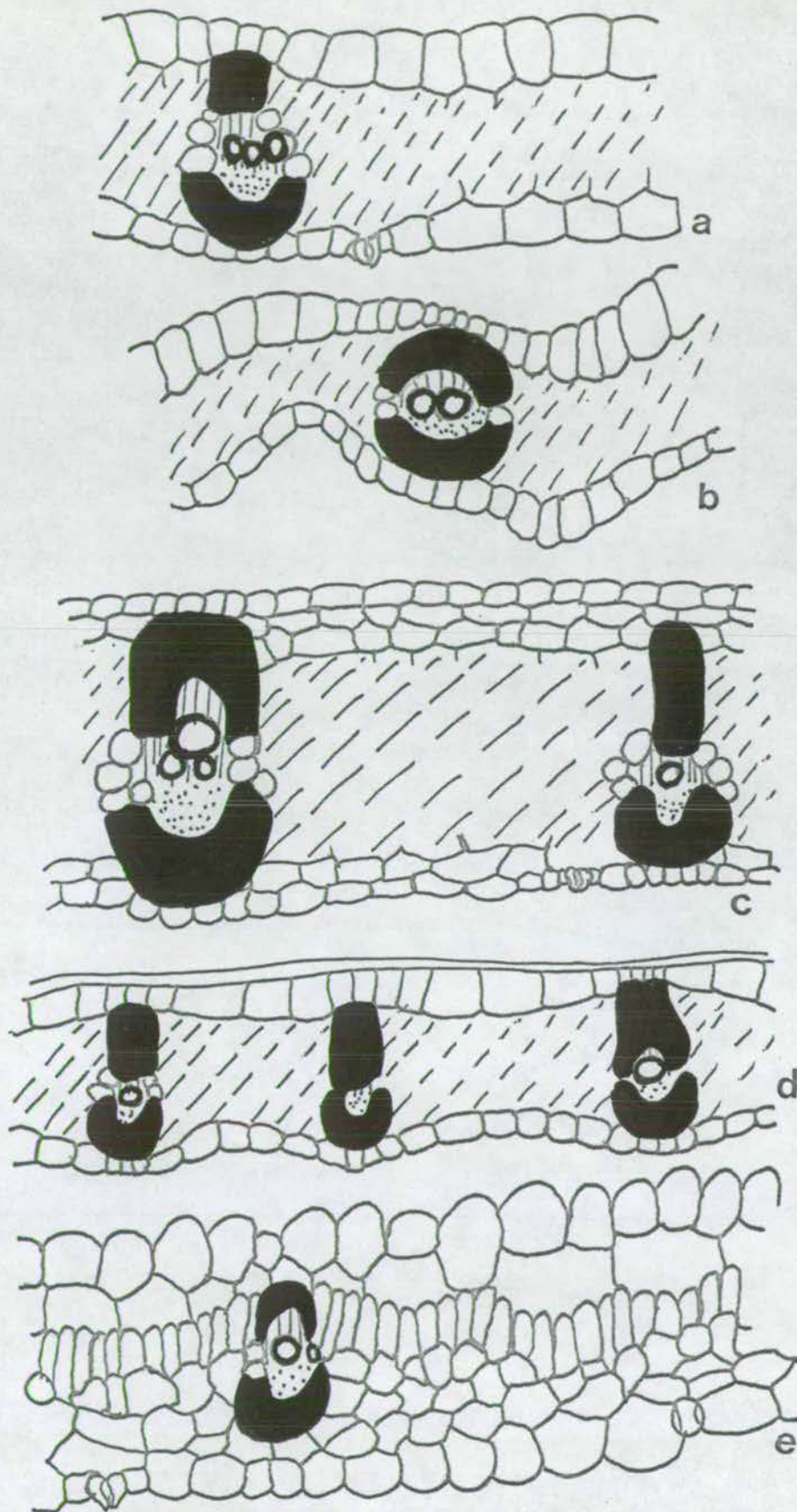


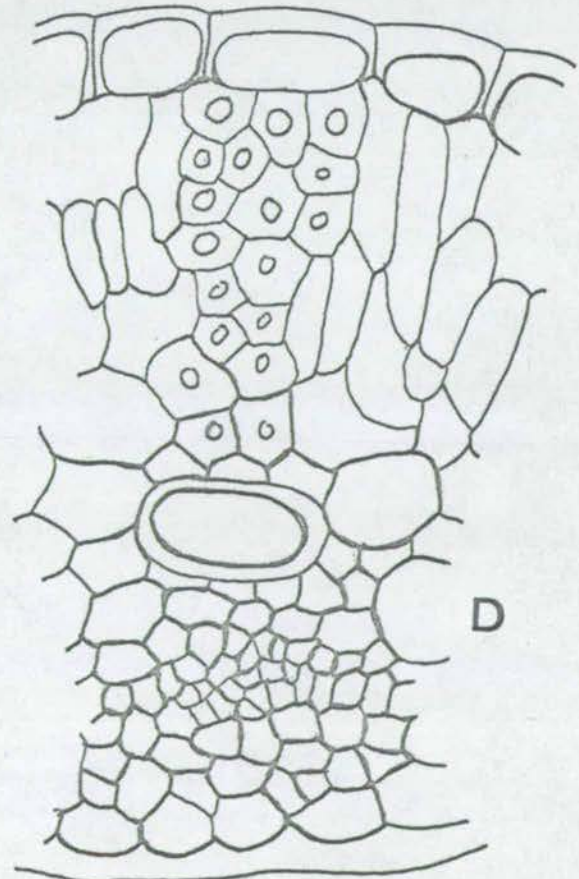
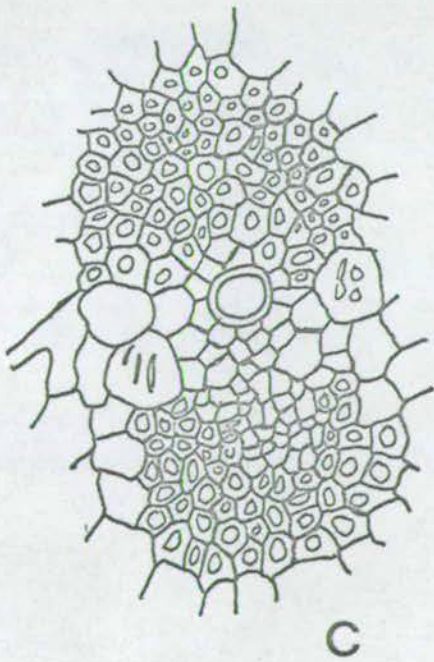
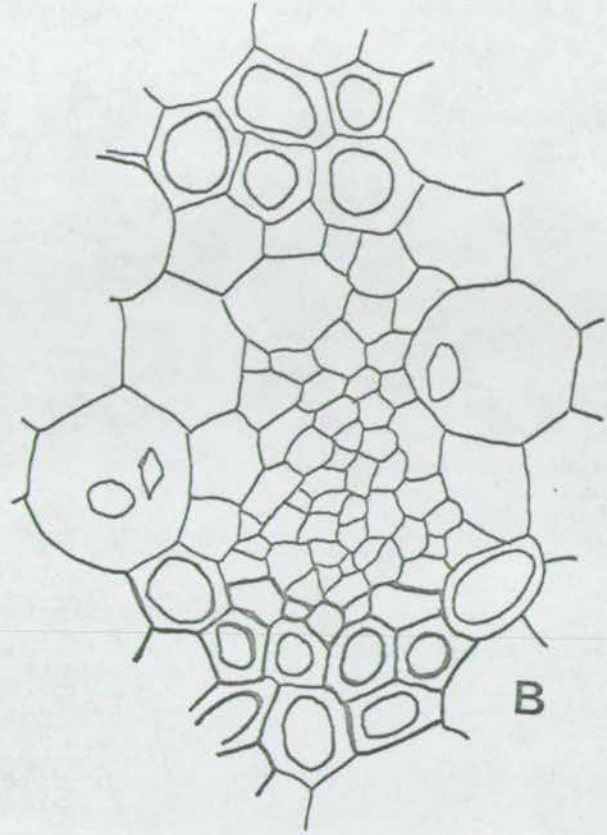
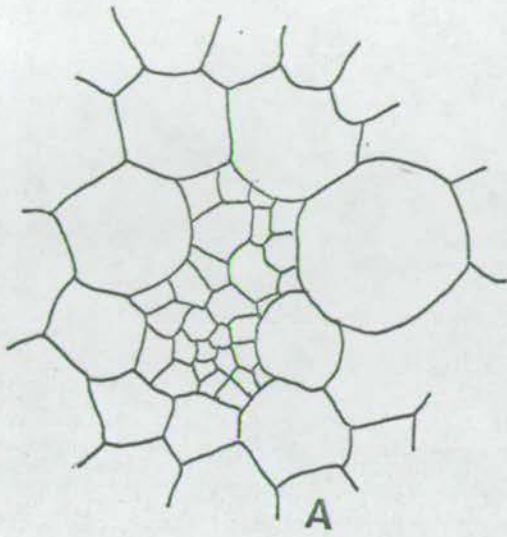
Fig.19

FIG. 20. TYPES OF VASCULAR BUNDLE

Explanation in the text.

- A. Camptandra latifolia (x680)
- B. C. latifolia (x 680)
- C. Zingiber incoptum (x180)
- D. Alpinia calcarata (x680)

Fig.20



about one to five cells wide through the mesophyll to both or either epidermises as in Alpinia calcarata (fig. 20.D). Where the bundle extension does not reach the epidermis, it may be connected to this by hypodermal cells which may be modified as smaller cells over the veins. There is variation in the extent of the buttressing to, or the independence of the vascular bundles and their sheaths from the epidermis and hypodermis of the lamina. In the majority of the genera in the family, the bundle sheaths of the larger vascular bundles are usually attached to either the epidermis or hypodermis or both surfaces. Examples are Alpinia allughas (fig. 21.E), Kaempferia aethiopica (fig. 23.c), and Alpinia pulchra (fig. 19.d). The sheath of the large bundles may reach the adaxial surface only, as in some species of Curcuma, Kaempferia, Burbridgea and Hedychium cylindricum. The sheath may be attached to the abaxial surface but not to the adaxial epidermis. Examples are found in Renealmia (fig. 21.A), Alpinia graminacea (fig. 21.B), A. sandaracae, A. sp., A. samoensis, Amomum repocense, A. ovoides, Aframomum humburgii and Riedelia sp. (Millar 14594). In the above species, the bundle sheath is separated from the hypodermal fibres above by mesophyll cells. Finally, the bundle sheaths may be more or less completely independent of the two surfaces and hypodermises. This type of bundle is common in the following genera, Scaphochlamys, Boesenbergia (fig. 23.a), Camptandra and some of the species of Kaempferia and Haplochorema. In these species, as was discussed on page 65, because of the more or less independence of the veins from the epidermises, the costal cells are not usually strongly modified on both abaxial and adaxial epidermises.

HYPODERMAL FIBRES (figs. 21 and 22).

Isolated fibres or fibrous strands were observed in the materials for

thirty seven out of about three hundred and five species examined during this study. These species are listed in Table 3.

These fibres occur either singly or in groups to form strands. They were found below the epidermis in the lamina and particularly associated either with the hypodermal layers or the palisade mesophyll cells. They occur either above the main veins (fig. 21.A,B; 22.A,B) in the hypodermal position vertically above the veins from which they are separated by assimilating tissue, and/or in the spaces between the veins (fig. 21.C,D,E; 22.B,C), in both or either hypodermises. These fibres or fibrous strands will heretofore be referred to as the hypodermal fibres. This term is deemed appropriate because, topographically, they are found more in the hypodermal layers, or where these are absent, they occupy positions similar to the hypodermis if the latter were to be present; and, moreover, because of ease of reference, and more particularly, to distinguish them from the more internal mesophyll fibres, which are not usually associated with the hypodermis, as in the Bromeliaceae (Tomlinson 1969, p. 252, 405).

Tomlinson (1956, 1969) reported the presence of these hypodermal fibres in Renealmia, Aframomum and Elettariopsis curtisii but he did not strongly refer to them as hypodermal fibres as such, but as "fibres in mesophyll". In this study, hypodermal fibres have been observed in the materials for thirty-seven species belonging to eight different genera including Renealmia and Aframomum. The fibrous strands which are separated from the large vascular bundles by the mesophyll cells are by far the commonest type seen in most of the species. These fibres usually occur as fibrous plates, consisting of from ten to twenty cells in width as seen in transverse sections (fig. 21 and fig. 22), and close to the hypodermis or epidermis as in Renealmia antillarum

TABLE 3. LAMINA HYPODERMAL FIBRES

<u>SPECIES</u>		<u>LOCATION</u>
1.	<u>Renealmia antillarum</u>	Adaxial
2.	<u>R. cabraei</u>	"
3.	<u>R. occidentalis</u>	"
4.	<u>R. bracteosa</u>	"
5.	<u>R. exaltata</u>	"
6.	<u>R. micrantha</u>	"
7.	<u>R. dermatopetala</u>	"
8.	<u>R. racemosa</u>	"
9.	<u>R. spicata</u>	"
10.	<u>R. polyantha</u>	"
11.	<u>R. sessiliflora</u>	"
12.	<u>R. ciliolata</u>	"
13.	<u>R. flocheri</u>	"
14.	<u>R. sp. (G. Zenker 525)</u>	"
15.	<u>R. sp. (H.H. Smith 2657)</u>	"
16.	<u>Alpinia sandarac</u>	"
17.	<u>A. bracteosa</u>	"
18.	<u>A. graminacea</u>	"
19.	<u>A. allughae</u>	"
20.	<u>A. sp. (B 4376)</u>	Adaxial
21.	<u>A. sp. (B 5221)</u>	"
22.	<u>A. sp. (B 5300)</u>	"
23.	<u>A. sp. (B 5289)</u>	"
24.	<u>Cenolophon oxymitrum</u>	Adaxial and abaxial
25.	<u>Anacardium ovoides</u>	"
26.	<u>A. repens</u>	"
27.	<u>A. dealbatum</u>	"
28.	<u>A. sp. (B 5337)</u>	"
29.	<u>A. sp. (B 4811)</u>	"
30.	<u>Aframomum humburgii</u>	"
31.	<u>A. daniellii</u>	"
32.	<u>Elettaria</u>	"
33.	<u>E. sp. (B 2085)</u>	"
34.	<u>E. sp. (B 2577)</u>	"
35.	<u>E. sp.</u>	"
36.	<u>Riedelia sp.</u>	"
37.	<u>Cyphostigma pedicellatum</u>	"

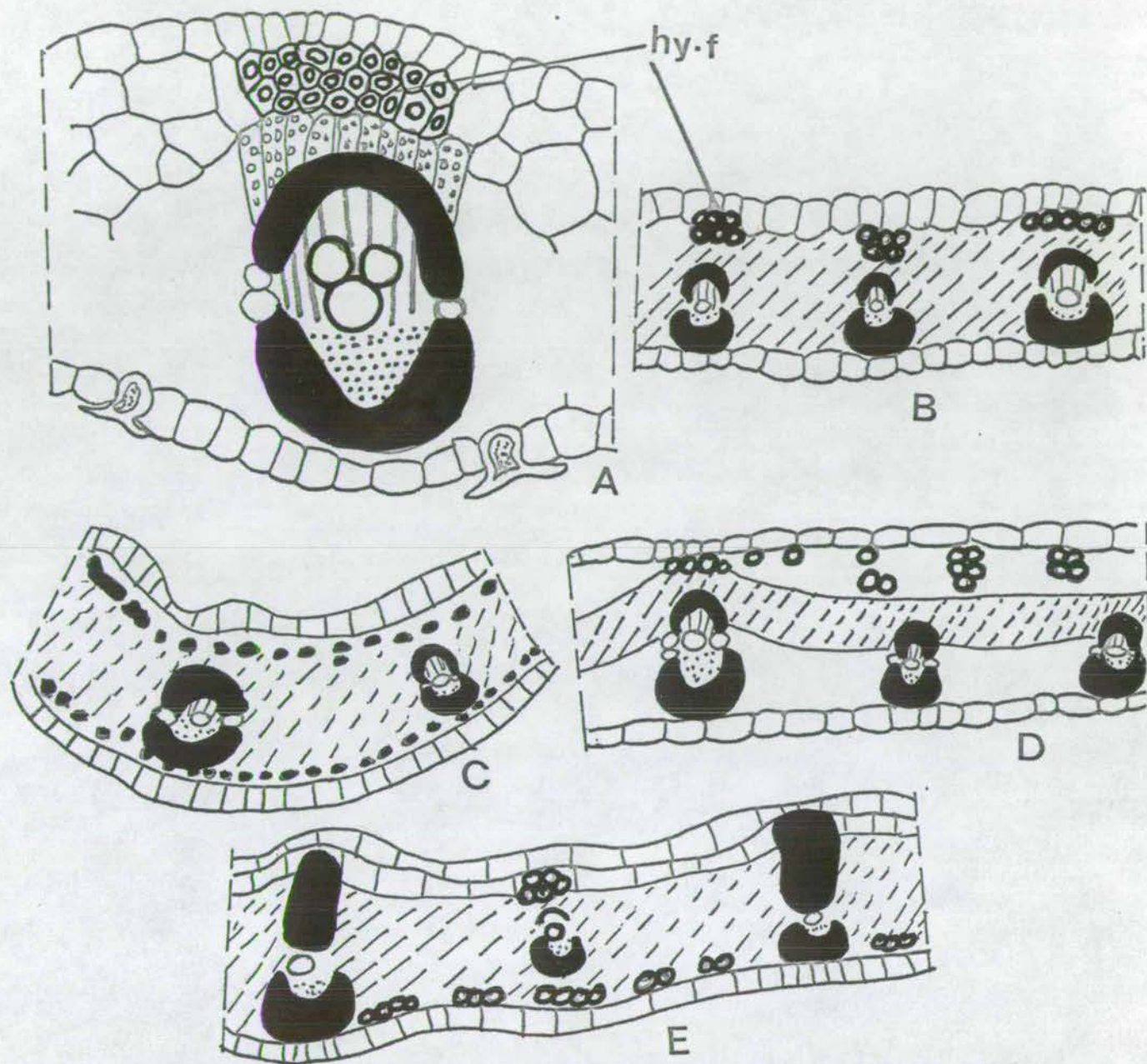


Fig.21

FIG. 21. HYPODERMAL FIBRES.

Explanation in the text.

- (A) Renealmia bracteosa. (x180)
- (B) Alpinia graminacea.
- (C) Cenolophon oxymitrum.
- (D) Alpinia allughas.
- (E) Aframomum humburgii.

Figures B - E x 31

hy.f = hypodermal fibres.

FIG. 22. HYPODERMAL FIBRES.

Explanation in the text.

- A. Renealmia antillarum.
- B. Aframomum humburgii.
- C. Alpinia allughas.

All figures x c. 340
hy.f = hypodermal fibres.

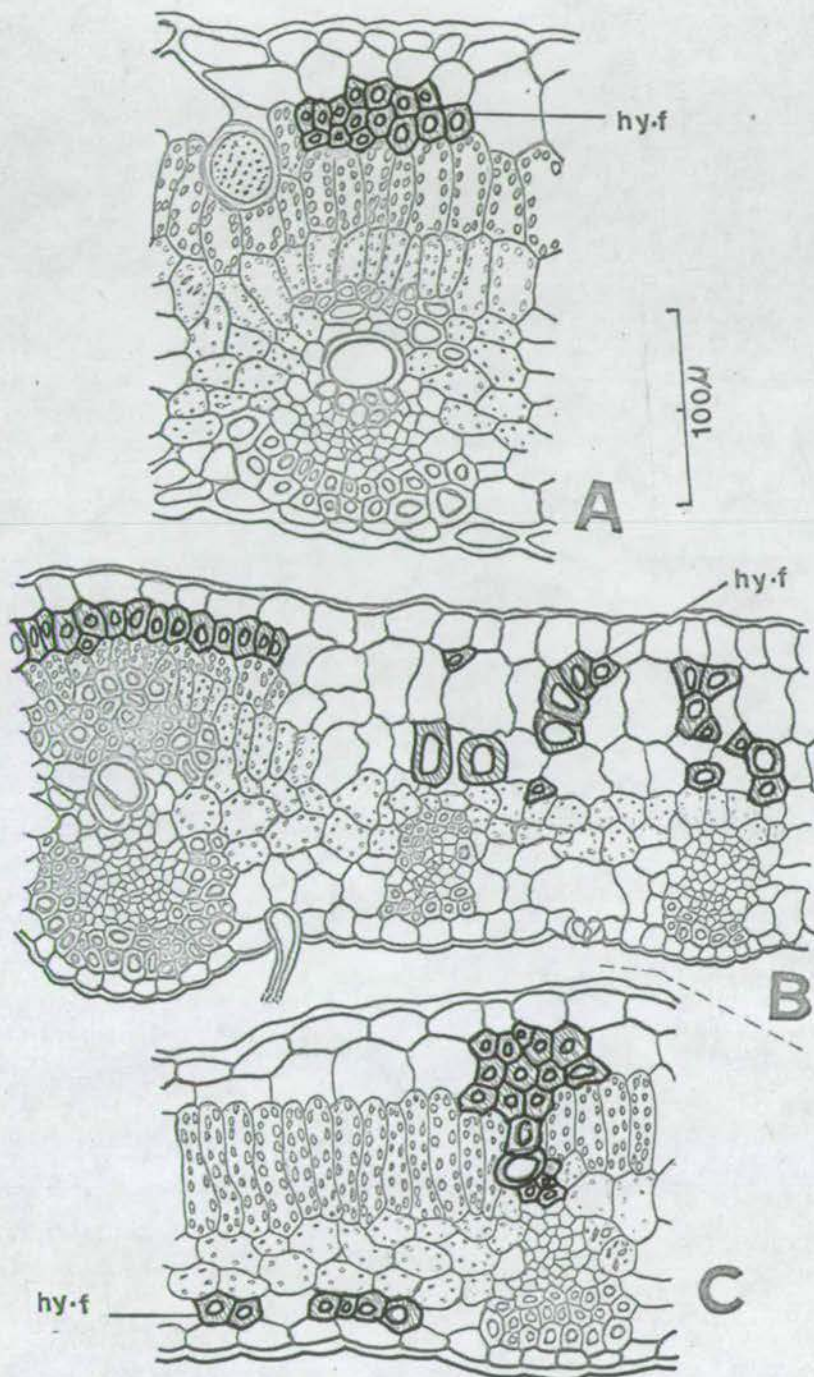


Fig. 22

(fig. 22.A) and Aframomum humburgii (fig. 22.B). However, isolated fibres similar to those reported by Tomlinson (1956) for Elettariopsis curtisii were observed in both or either hypodermis or below the epidermis in the following species:- in both adaxial and abaxial positions in Cenolophon oxymitrum (fig. 21.C), adaxial in Alpinia allughas (fig. 21.D), A. sp. (B 5221) and Aframomum humburgii (fig. 21.E; 22.B). These fibres occur singly or in groups varying from one to several cells. They are not confined to the vertical positions above the veins only, but are interspersed among the hypodermal or palisade cells in both or either surfaces. In Aframomum humburgii, they are found scattered in the two adaxial hypodermal layers. These fibres recall the foliar sclereids found in some dicotyledonous families.

In longitudinal section, or from macerated tissue, the fibres of the fibrous plate above the veins appear as true sclerenchymatous fibres. They are long, acicular, they may be sharply pointed or blunt, and their walls are very thick and occasionally lignified. The isolated fibres are very similar to the above but they usually are distinct in surface view (Plate 4.C) from adjacent parenchymatous cells of the hypodermal or palisade layers. The fibres above the veins are very similar in all their features to the intercostal fibres too.

The terminology now suggested for the hypodermal fibres as distinct from the fibres of the bundle sheath and the internal mesophyll fibres may be debatable. The comparison of the hypodermal fibres, particularly those vertically above the veins, with the fibrous plates which pass to the adaxial epidermis through the mesophyll of some genera or species, e.g. Alpinia calcarata and Plagiostachys paradoxa, might tend to suggest that the group of fibres, separated from the large veins by the assimilating tissue, belong to

the bundle sheath. The hypodermal fibres referred to above always appear to be more strongly developed towards the hypodermis (fig. 22.C) than nearer the vascular bundles. They are usually distinct from the fibrous plate of certain genera where there is a stout and almost consistent development of the bundle sheath extension to the epidermis as in Alpinia samoensis (fig. 19.), Zingiber, and Roscoea. The argument here is that the fibrous plates which are more strongly developed towards the epidermis might be a transition step towards the complete isolation of the hypodermal plates from the bundle sheath. It does suggest a hypodermal or mesophyll origin for these fibres. Although living materials were not available for the developmental studies on these fibres, such study might contribute usefully to this discussion. Tomlinson (1956), suggested that these fibres might be of mesophyll origin. Pfitzer (1872) had long ago interpreted the hypodermis as being differentiated from the mesophyll. The major support for this suggestion comes from the fact that, in this study, the hypodermal fibres are not confined only to the adaxial vertical position above the veins, but along with these, they often occupy the spaces in between the veins where there are no vascular bundles beneath them, (fig. 21.C-E; 22.B,C). This suggests that at least the isolated fibres are specialised cells which have been differentiated from the hypodermis or mesophyll along a line which is strongly towards the sclerenchymatous fibres. Since the hypodermis itself has an undisputed mesophyll origin, any cells which are further differentiated from the hypodermis must have had a mesophyll origin through its evolution. Therefore, it is suggested that the term 'hypodermal fibres' might be applicable to these fibres, at least, topographically.

MESOPHYLL.

The relative thickness or height of the assimilatory tissue to that of the entire lamina varies with the species, the number of hypodermal layers, and the size of the epidermal and hypodermal cells on both surfaces. In the tribes Globbeae, Alpinieae and Zingibereae (Zingiber) and some genera of Hedychieae, where the hypodermal layers vary between 0-1 on both or either surface, the assimilatory tissue may occupy more than half of the height of the lamina, e.g. Kaempferia aethiopica (fig. 23.c). Where there are two or more hypodermal fibres on both surfaces and the cells are large, the assimilatory tissue may be less than half the height of the lamina as in Scaphochlamys, Boesenbergia (fig. 23.a), Kaempferia (fig. 23.d). If the hypodermal layers are developed on one side only, the assimilatory tissue is confined to the other side of the lamina as in Globba (fig. 23.e). The condition in Scaphochlamys, Kaempferia, Boesenbergia and to some extent in Curcuma where the assimilatory tissue is narrow and restricted to the centre of the lamina, is probably what was referred to as 'centric mesophyll' for Zingiber capitatum by Solereder and Meyer (1930).

The lamina of the African Kaempferias differ from the Asiatic Kaempferias in that the hypodermis is absent or feebly developed and consequently the assimilatory tissue extends from the abaxial to the adaxial epidermis (fig. 23.c). Whereas in the Asiatic Kaempferias, the hypodermis is well developed and the mesophyll is more or less centric (fig. 19.e; 23.a,d).

The lamina is dorsiventral, the mesophyll is differentiated into the adaxial palisade and abaxial spongy layers, except to a lesser extent in Scaphochlamys and Boesenbergia (fig. 23.a).

The number of layers of the palisade mesophyll varies from one to three

FIG. 23. TRANSVERSE SECTIONS THROUGH THE LAMINA - MESOPHYLL.

Explanation in the text.

- a. Boesenbergia plicata (x180)
- b. B. sp. (B 4927) (x100)
- c. Kaempferia aethiopica (= Gienkowskya aethiopica) (x180)
- d. K. elegans (x100)
- e. Globba atrosanguinea (x180)
- f. Burbridgea pubescens (x180)

ab. pal. = abaxial palisade cells;

o.c. = oil cells; si. = silica bodies; st. = stomata.

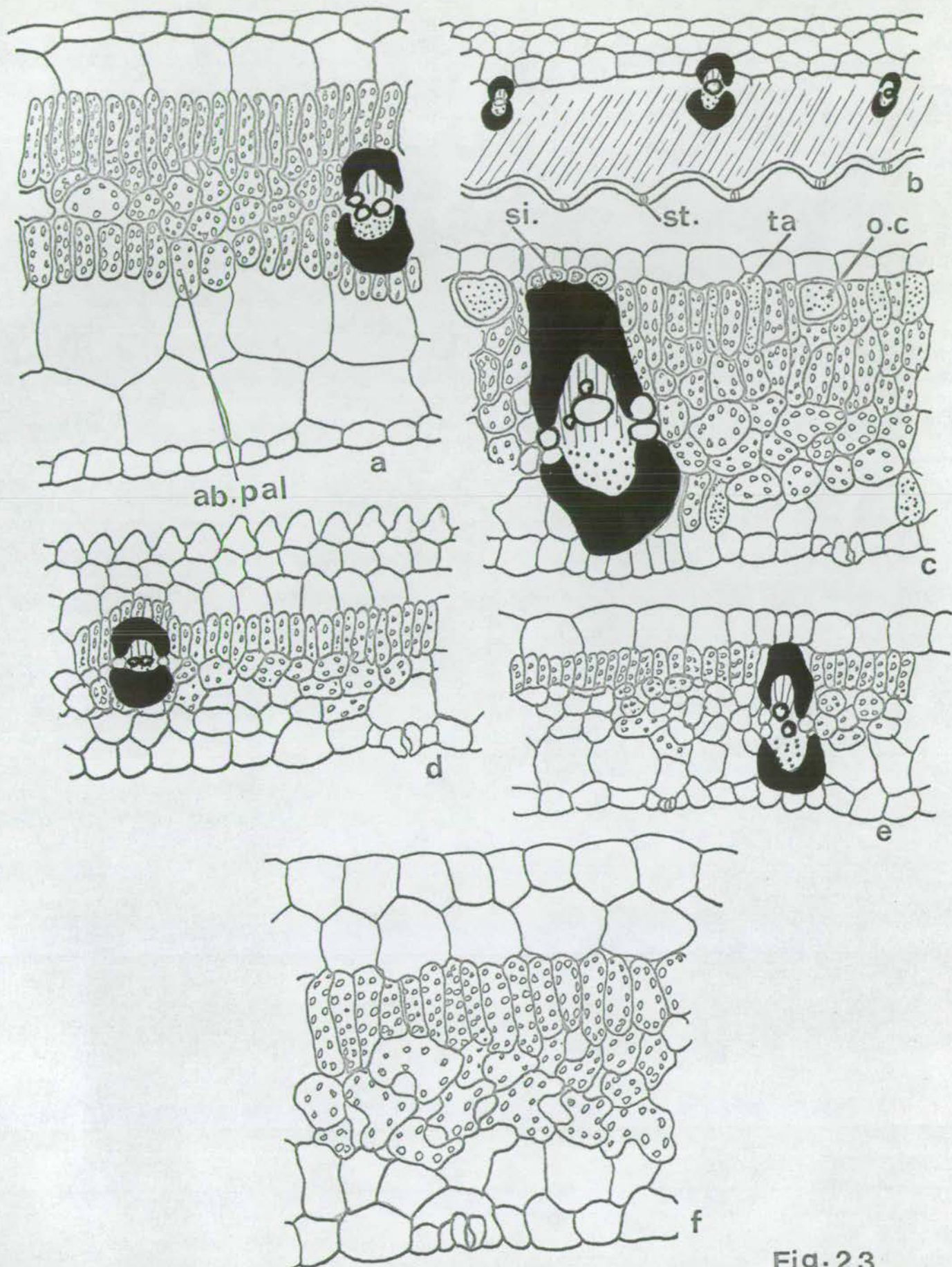


Fig. 23

The palisade cells are cylindrical, elongated vertically, about two to three times as high as broad, rounded or slightly conical on both sides. These palisade cells are variously compacted and they may be interspersed by tanniniferous cells which are similar in shape and size, as in Kaempferia aethiopica. The palisade cells may be completely over-shadowed by the colour of the tanniniferous cells as in Plagiostachys where tanniniferous cells are numerous. The presence of the tanniniferous cells in the palisade mesophyll is a characteristic of most genera in the family, particularly in the tribes Zingibereae and Alpinieae. The palisade cells usually contain abundant chloroplasts and sometimes crystals of calcium oxalate. In the genera where there are more than one layer of palisade mesophyll, the abaxial layer/s pass almost imperceptibly into the spongy cells below.

The spongy mesophyll also varies from one to four layers. It is usually composed of two types of cells depending on their arrangements. (i) Spongy mesophyll with rather closely compacted cells, round or elliptic and they leave smaller intercellular spaces in between them. Examples are found in Curcuma, Kaempferia (fig. 23.d). (ii) The cells may be loosely arranged as in Boesenbergia plicata (fig. 23.e). The cells may be round or branched and in some cases the arms may radiate from a central axis. These cells leave abundant air spaces in between them. Examples are, Burbridgea pubescens (fig. 23.f), Camptandra and Renealmia.

A slightly different situation to that described above is observed in a number of species of Scaphochlamys and Boesenbergia. In these species, in addition to the adaxial palisade cells, a palisade-like layer is present abaxial to the usually 1-2 layers of spongy mesophyll (fig. 23.a). The adaxial palisade layers and the abaxial palisade-like cells sandwiched the

spongy cells. The abaxial palisade-like cells are not equally differentiated in the different species of the two genera. They are definitely obvious in Boesenbergia plicata (fig. 23.a) and Scaphochlamys perakensis. In these species, the mesophyll approaches an isobilateral structure except that the spongy cells are distinctly differentiated. Solereder and Meyer (1930) reported these cells for some species of Scaphochlamys and this has been seen in a number of species of this genus. As mentioned above, these abaxial palisade-like cells are well differentiated in Scaphochlamys perakensis but absent in S. kunstleri.

The lamina of Scaphochlamys and Boesenbergia is usually held more or less erect but with adaxial surface still more exposed to the sunlight than the abaxial surface. It is not, therefore, surprising that the mesophyll differentiation approaches the isobilateral condition common in the Gramineae and Iridaceae.

CELL INCLUSIONS.

SILICA.

Silica occurs in two forms in this family. It could occur as (i) discrete bodies of measurable sizes inside cells or fibres; such cells or fibres containing silica bodies are referred to as stegmata (fig. 25.A-E; Plate 4.b). (ii) Silica may also occur as silica sand; these are loose granular or coarse deposits of very variable sizes occupying the whole cell or part of it (fig. 24.d-f).

STEGMATA.

Stegmata may occur in the epidermal cells in continuous or interrupted parallel series above the veins on both or either surface of the lamina, as

in Alpinia mutica, A. allughas (fig. 24.b), Elettaria surculosa (fig. 24.a), The cell walls of the stigmata may be thickened in a U-shaped or circular manner, as in Alpinia allughas (fig. 24.b) and Geostachys taipingensis, or the walls may not be differently modified from those of the adjacent cells as in Alpinia mutica and Elettaria surculosa (fig. 24.a). Epidermal stigmata are commonly found in most, but not all, species in the tribe Alpineae. Stigmata are found in the epidermal cells apart from those over veins in Rhynchanthus sp. (Keenan 3107) (fig. 24.c).

Another type of stigmata are those that occur internally in specialised fibres or cells adjacent to the bundle sheath fibres, or may be found occasionally in some other cells of the internal ground tissue of the lamina and sheath as in Kaempferia aethiopica (Plate 4.B; fig. 25.A-B). The fibres containing these silica bodies are rather specialised in that their lumen is divided into compartments and each compartment contains one silica body (Plate 4.B; fig. 25). The U-shaped thickenings in the walls of these fibres, without doubt, gave rise to the compartments in the lumen. This type of stigmata is rare in the Alpinieae except where they occur occasionally as in Alpinia pahangensis. The first report of the occurrence of stigmata in the tribe Hedychieae was that of Tomlinson (1956) for Kaempferia kirkii (= Cienkowskyia kirkii). In this study, stigmata have been observed in six species of African Kaempferia (Cienkowskyia), and these bring the number of the species of Cienkowskyia with stigmata, to seven out of about twelve known species of this African genus. Stigmata are not present in any of the Asiatic species of Kaempferia. Internal stigmata have also been observed for two species of Globba, viz. G. leucantha, and G. pendula. Another specimen G. sp. (B 4885) in which these stigmata are also found is very similar in all its anatomical features

FIG. 24. CELL INCLUSIONS - EPIDERMAL STEGMATA
AND SILICA SANDS

Explanation in the text.

- (a) Elettaria surculosa (x 680)
- (b) Alpinia allughas (x 180)
- (c) Rhynchanthus sp. (Keenan 3107) (x 680)
- (d) Alpinia rufa (x 180)
- (e) Zingiber puberulum (x 180)
- (f) Globba atrosanguinea (x 180)
- (g) Scaphochlamys Kunstleri (x 180)

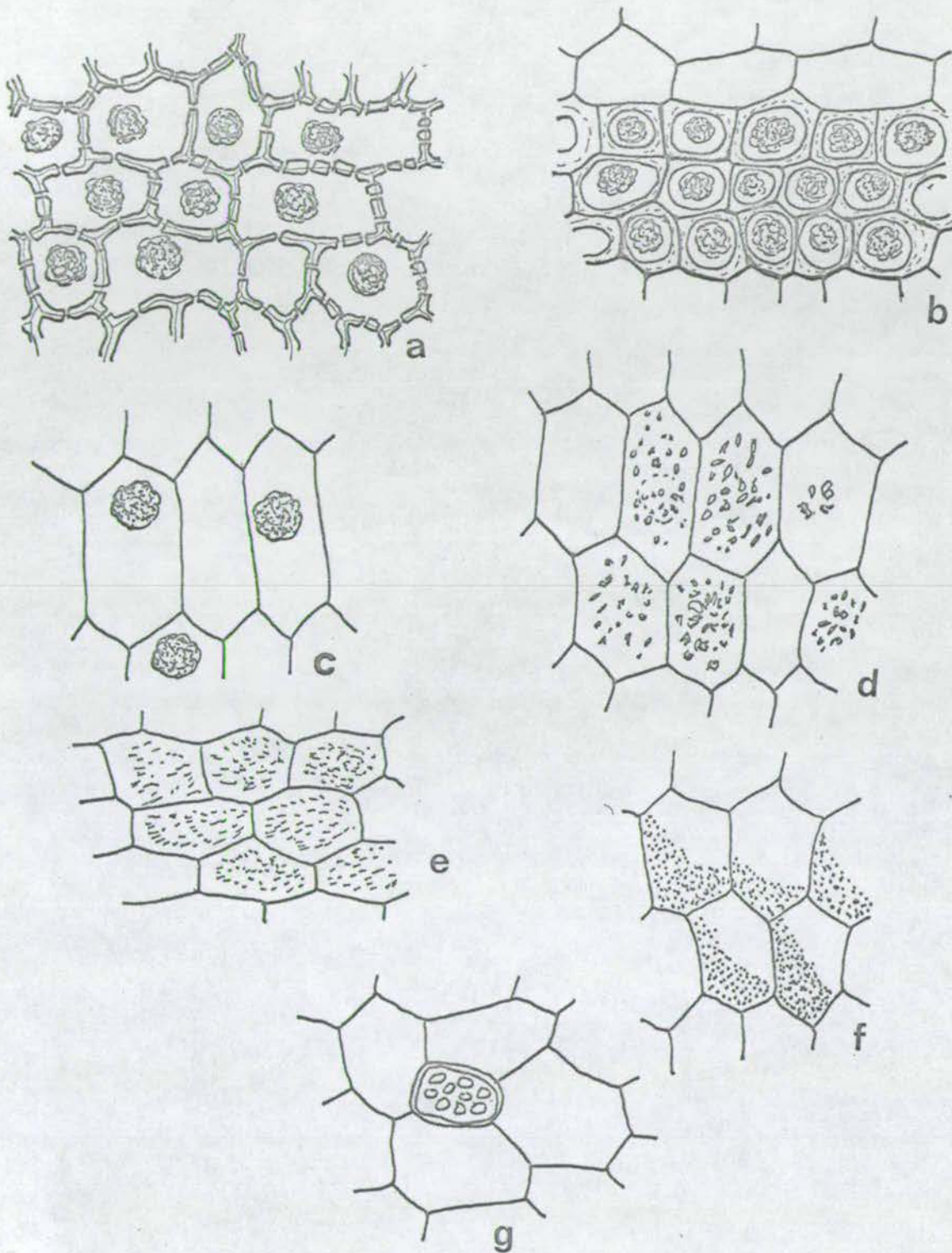


Fig-24

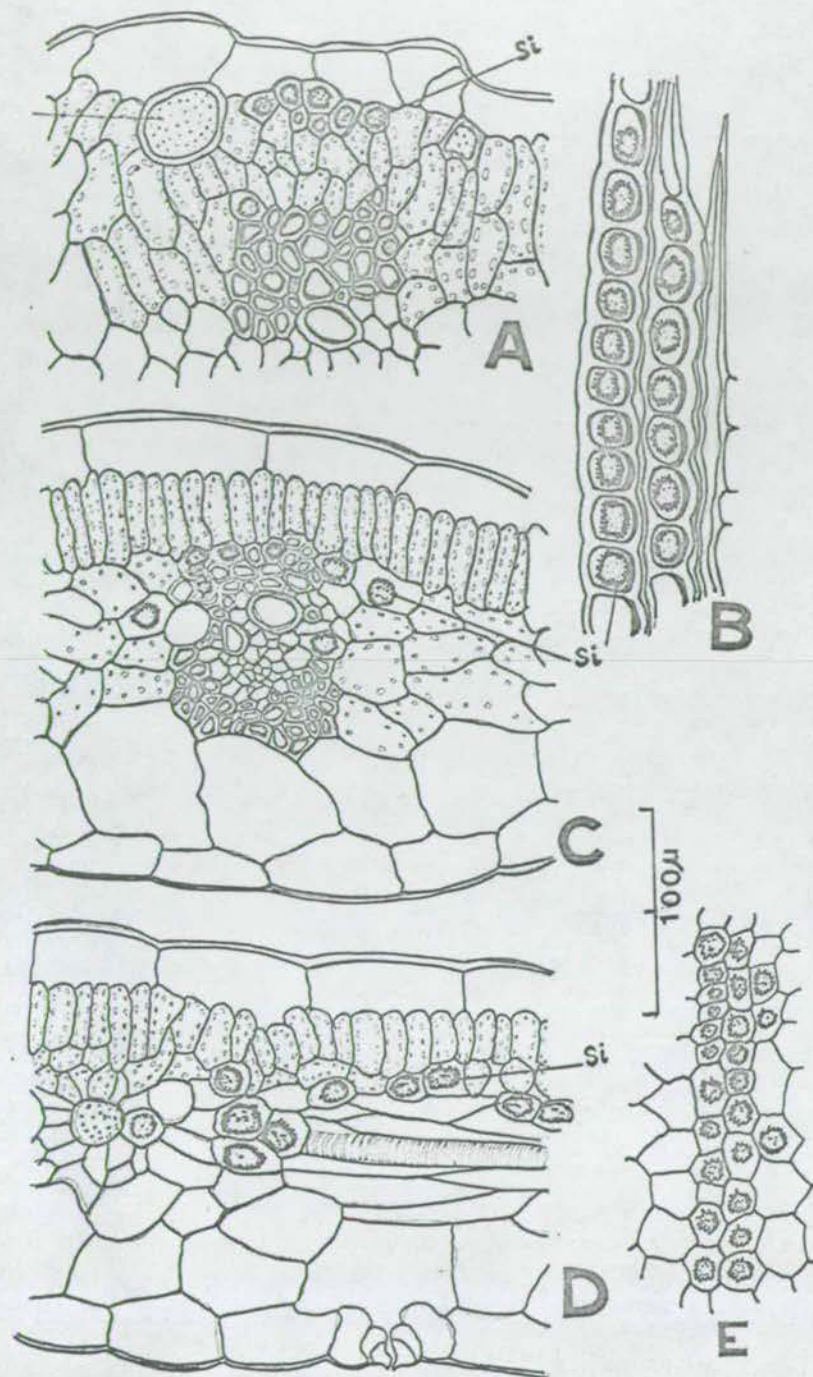


Fig-25

FIG.25. TRANSVERSE SECTIONS THROUGH PART OF THE LAMINA SHOWING THE INTERNAL STEGMATA.

Explanation in the text.

- A. Kaempferia aethiopica (=Cienkowskya aethiopica);
 B. K.aethiopica; C,D. Globba leucantha;
 E. Amomum cardamomum.

si.= silica bodies.

to G. leucantha, and it may belong to this species.

It is noteworthy that, in the species of African Kaempferia (Cienkowsky) and Globba mentioned above, only internal stigmata are found, and not the epidermal stigmata which are common in the species of the tribe Alpinieae. Furthermore, these internal stigmata occur in the lamina and sheath of the African Kaempferia and therefore make these species easily identifiable, even when fragmentary materials are available.

The individual silica body is usually spherical or slightly oblong with an irregular surface which may be sharply, or less sharply pointed. The size of the silica bodies varies in the different species and may also vary on the same lamina. Tomlinson (1956) gave the measurements of the diameter of the silica bodies for Alpinia javanica 5 μ , Elettaria cardamomum and Geostachys taipingensis 5 μ . After the preliminary measurements of these silica bodies, it is found that the range of average diameter in most species overlaps, and this makes the distinction between two species on this character, difficult. The measurements of the silica bodies are probably of some value below the species level, but they cannot be used at the generic level.

SILICA SAND.

As mentioned above (page 120), silica may occur as loose granular or coarse particles in cells. They are particularly abundant in the epidermal and mesophyll cells of some species, e.g. Alpinia rufa (fig. 24.d). They have been reported in the epidermal cells of Alpinia bracteata, Catimbium speciosum, and in the intercostal region of the epidermis in Alpinia javanica, A. bracteata, Catimbium speciosum, and Geostachys taipingensis, and in the mesophyll of Renealmia and Globba bulbifera. Loose granular silica sand is abundant in the parenchyma cells near the bundle sheath in the lamina of

Zingiber puberulum (fig. 24.e), and Globba atosanguinea (fig. 24.f). It appears that silica sand is of wide occurrence in the family, whereas true silica bodies are more or less restricted to the tribe Alpinieae, except the species of African Kaempferia (Cienkowskya) in the tribe Hedychieae and two species of Globba in the Globbeae.

In the epidermal cells of Alpinia rufa (fig. 24.d), crystal-like silica deposits or granules are very abundant. Some of these granules are of moderate sizes. Sometimes, these granules may be partially agglomerated together in a manner almost resembling the true silica bodies (fig. 24.e). Many of these granules are also found in the same cells as the true silica bodies. It might be true, as suggested by Solereder and Meyer (1930), that the loose silica sands were formed as a result of the breakdown of the larger bodies. At the same time, from the pattern of distribution of these granules in Alpinia rufa and Catimbum speciosa, where they tend to agglomerate together, it could be that these granules join together to form the larger bodies.

CALCIUM OXALATE (fig. 26).

Crystals of calcium oxalate were observed in all the plants examined, although the abundance of these crystals varies in the different species. These crystals were particularly easily observable in the epidermal preparations and transverse sections of the lamina, petiole and sheath stained in Delafield's haematoxylin.

The calcium oxalate crystals vary very much in shape in the different species, even among crystals in the same cell. According to Tomlinson (1956), these crystals of calcium oxalate were referable to rhombohedral system. In shape they could be rhombohedral, prismatic, tabular, cuboid, rod-shaped, as

simple needle-like crystals (raphide or raphide-like), or as druses (fig. 26.E). Some crystals appear as 'flakes' or 'pellets', where they are flattened and one of the sides is very narrow (fig. 26.B), some also appear 'x-shaped', e.g. raphide-like druses in Burbidgea pubescens (fig. 26.E), and few others may appear as 'V' shaped (fig. 26.D,E). These various shapes were observed in the different species.

In some species there are crystal sands which are made up of minute crystals. These often resemble the silica sand described on page although their characteristic birefringence of the individual crystals of calcium oxalate distinguishes the latter from the silica sand. These crystal sands are common in most species of Roscoea, and have been observed in the hypodermal cells of Burbidgea pubescens. In Globba, as was reported by Tomlinson (1956), simple large crystals are commonly found in each cell (Plate 7.f). These crystals have been observed in most of the species examined and may be diagnostic for Globba.

Crystals of calcium oxalate are more abundant in the assimilatory tissue to which they are associated (Tomlinson 1956). The abundance of crystals decreases gradually from the lamina to the petiole, sheath and stem, where they become fewer. There are some exceptions, however, such as in Brachychilum horsfieldii where Tomlinson observed these crystals of calcium oxalate in abundance in the root and rhizome.

The crystals of calcium oxalate vary very much in shape and none of the genera is characterised by any particular shape. It is, therefore, doubtful whether the crystals could be of use for generic determination, except probably for Globba.

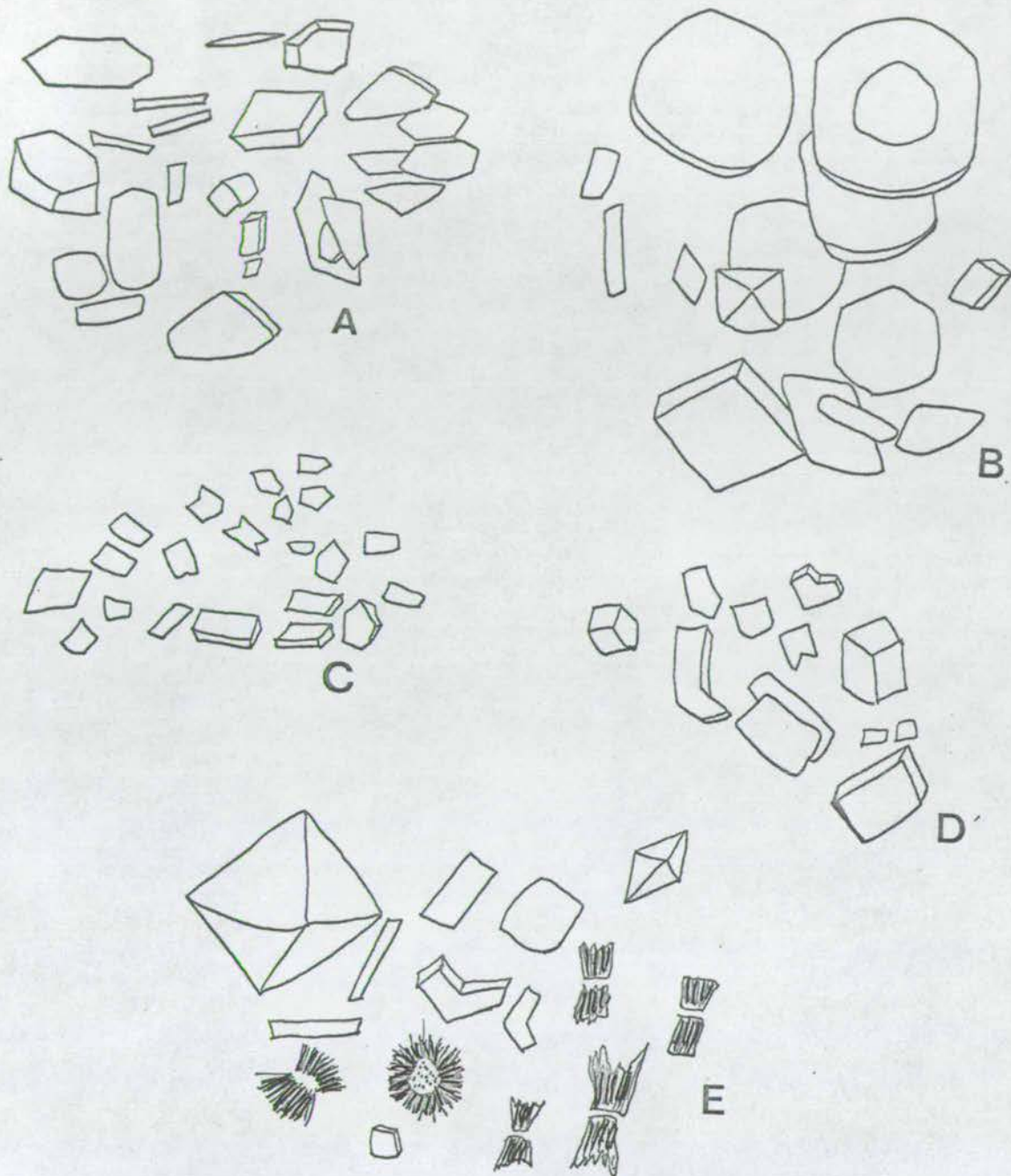


Fig. 26

FIG. 26. CRYSTALS.

Explanation in the text.

- (A) Zingiber officinale.
- (B) Z. sp. (Woods 579).
- (C) Globba atrosanguinea.
- (D) Hedychium gardnerianum.
- (E) Burbidgea pubescens.

All figures x c.680)

TANNINS.

The term tannins refers, in a wide sense, to a variety of heterogenous phenolic substances or derivatives, which are usually related to glucosides Esau 1953). Tannins are present in all the plants examined for the family in this study.

Tannins occur in different parts of the plant and are particularly abundant in the lamina. They occur in the cells of the different layers of the lamina as seen from transverse sections, but they are usually more frequent in the palisade mesophyll. In this position, they occur in cells which are similar in shape to the palisade cells, although they may be larger than the latter. The colour of the tanniniferous cells usually overshadows the chlorenchyma cells in the palisade layer, as in Plagiostachys and Kaempferia aethiopica (Cienkowskya aethiopica). Tannin also occurs in elongated parenchyma cells in the internal tissues of petiole, sheath, stem and roots. These parenchyma cells usually form a connected series of tannin cells which appear similar to ducts or laticifers (Tomlinson 1956). In some cases the cells are short and scattered in the hypodermal layers as in Zingiber capitatum. Tannin occurs in the individual cells both of the epidermal cells and in the internal tissue. In most species of Zingiber, such cells are abundant in the ligule.

There are some differences observed in the colour of the tanniniferous substances in the different species. The unstained transverse sections of the lamina, sheath, stem and root, show these colours very well. The substances may be coloured dark brown as in Alpinia allughas and A. graminacea, golden brown as in Kaempferia aethiopica (Cienkowskya aethiopica) and Plagiostachys sp. (B 5429).

The chemistry of these tanniniferous substances in the Zingiberaceae is not well known, and their investigation might be rewarding if made. However, these substances appear to be soluble in water, as they are extracted into the boiling water during the revival of the herbarium specimens. The strong aromatic smell that is characteristic of this family (excluding Costaceae), might not be due only to the oily substances found in these plants as suggested by Tomlinson (1956), but may be due to both the oily and tanniniferous substances.

OIL CELLS.

The presence of oil cells is a characteristic feature of the Zingiberaceae. It distinguishes this family from others in the order and from the former subfamily Costoideae (Costaceae, sensu Tomlinson 1969). Oil cells have been observed in all plants examined.

Oil cells are easily recognisable because of their size, which is usually smaller than the surrounding cells and/or by their homogenous amorphous or granular substance they contain. The Lugol's iodine test enables them to be studied easily. This substance or substances, may be coloured, in which case they are easily distinguished from the surrounding cells. In shape, the oil cells may be spherical, rectangular or isodiametric, as seen from the surface view of the epidermis (fig. 24.g) and from the transverse sections of lamina (fig. 25.A); occasionally, they may be elongated anticlinally as was reported by Tomlinson (1956) for Hornstedtia scyphifera. The oil cells in the hypodermis resemble the hypodermal cells except that they are usually smaller and contain colouring substances. The oil cells in the epidermis may become compressed by the adjacent cells, and the shape may become cubical or

rectangular as seen in surface view.

The walls of the oil cells are suberized but the Sudan IV test does not usually confirm this. The microchemical test of the cell walls made with chlor-zinc-iodide and 70% sulphuric acid confirms the presence of suberin. The cell walls of the oil cells turned yellow, whilst those of the adjacent cells gave a blue colour, which is characteristic of cellulose. The earlier workers, who studied the oil cells in some details, i.e. Biermann (1898), Zacharias (1879) and particularly Berthelat (1893), recognized two lamellae in the oil cells. According to them the outer is suberized and the inner made up of cellulose. In this study, these layers were not observed and it may be that other microchemical tests are needed for their confirmation. An electron microscopy study of these oil cells may yield valuable information that is difficult to obtain with the light microscope.

The contents of the oil cells are believed to be 'resin' substances (Tomlinson 1956), and as with the tannins, thorough investigations of the chemical properties and significance of these substances are much needed. As seen in either surface view or transverse sections, the contents of the oil cells may appear homogenous, amorphous or granular, and sometimes the content may be broken into sizeable droplets (fig. 24.g).

The distribution of the oil cells have been discussed in detail, by Tomlinson (1956). The following is a summary of the distribution. Oil cells are present in almost all the parts of the plant in the Zingiberaceae, although they may be more abundant in any one part than the other. Oil cells are frequent in the abaxial epidermis and both hypodermal layers of the lamina. Tomlinson (1956) observed oil cells in the adaxial epidermis of only one Kaempferia, these cells have also been observed in the adaxial epidermis of

the following species: Kaempferia rotunda, Kaempferia aethiopica (fig. 23.c), and Boesenbergia sp. (B 4900). Although the oil cells are infrequent in the adaxial epidermis, these are probably never completely absent. Oil cells are abundant in the mesophyll cells of the lamina. They are present in the epidermis of the petiole and sheath to almost the same frequency as in the lamina epidermis. Internally, they are fewer among the chlorenchyma cells surrounding the air canals in the sheath and petiole. Oil cells may be numerous and occasionally mixed with tannin cells in the cortex of the rhizome and root, although they are usually fewer in the latter.

STARCH GRAINS.

For the study of the starch grains in this family, attention is concentrated on the rhizome and root tubers, because these organs contain a greater abundance of mature starch grains than in any other part of the plant. The starch grains, as usual, gave positive iodine (KI) reactions.

The starch grains are simple, that is, they bear one hilum each. This hilum is almost always eccentric, i.e. it is usually located at or near the projecting beak at one end of the grain (fig. 27.E). In some cases, as in some of the grains in Camptandra latifolia (fig. 27.C), the hilum may be centric. The beak may be rounded or blunt as in Amomum hewithii (fig. 27.G), and Alpinia mutica, or sharply pointed as in Alpinia calcarata (fig. 27.J). Compound starch grains with two or three hilia are very rare, as was suggested by Tomlinson (1956), and were not observed in this study.

The starch grains usually occur singly. That is, each distinct and separated from the rest although may be housed within a cell. In some species, e.g. Amomum cardamomum (fig. 27.F), A. hewithii and Alpinia mutica (fig. 27.I), two, three or more grains may be fused together. The pattern of

the separating walls between these grains appears to suggest that this type of grains are almost like the compound grains with two or more hilum. Some of these fused grains when they separate bear some depressions indicating earlier closeness to other grains (fig. 27.F-I).

The laminations usually run in a concentric pattern round the hilum. These laminations are quite visible in some species and may not be distinct in some others.

The shape of the starch grains varies in the different species and may be constant for a particular species. But the differences in shape between different species are usually too small to be useful as a diagnostic character. Generally, the grains are flattened, and the shape in surface view may be circular, oval, elliptical, oblong (fig. 27.A-K), but where they are slightly flattened, it may be spherical, oval, cylindrical or ellipsoidal (fig. 27.A-K). The shape of the starch grains in the Alpinieae (fig. 27.F-I), with one end which is usually almost straight, concave or convex, may be very useful for separating the tribe from others where this type of grain is rarely found. The shape of the starch grains of some species in the Alpinieae, e.g. Cenolophon sp. (B & W 2268), may sometimes be similar to those in the other tribes as in Boesenbergia and Hedychium (fig. 27.A-D).

There is, however, a considerable variation in the size of the starch grains in the different species, and also among the starch grains of the same species. The largest grains measured in this study are those of Alpinia calcarata (fig. 27.J) with the following dimensions: $57.5 - 60 \mu \times 60 - 62 \mu$, and the longest recorded was in Zingiber officinale (fig. 27.E) with a length, from the hilum to the distal end, measuring up to 75μ .

As mentioned earlier, starch grains are abundant in the rhizome and storage

FIG. 27. STARCH GRAINS
Explanation in the text.

- A. Boesenbergia sp. (B 5146)
- B. B. sp. (B 5548)
- C. Camptandra latifolia.
- D. Hedychium greenii.
- E. Zingiber officinale.
- F. Amomum cardamomum.
- G. A. hewithii.
- H. A. sp. (B 2477)
- I. Alpinia mutica.
- J. A. calcarata
- K. Cenolophon sp. (B 2268)

All figures x 680

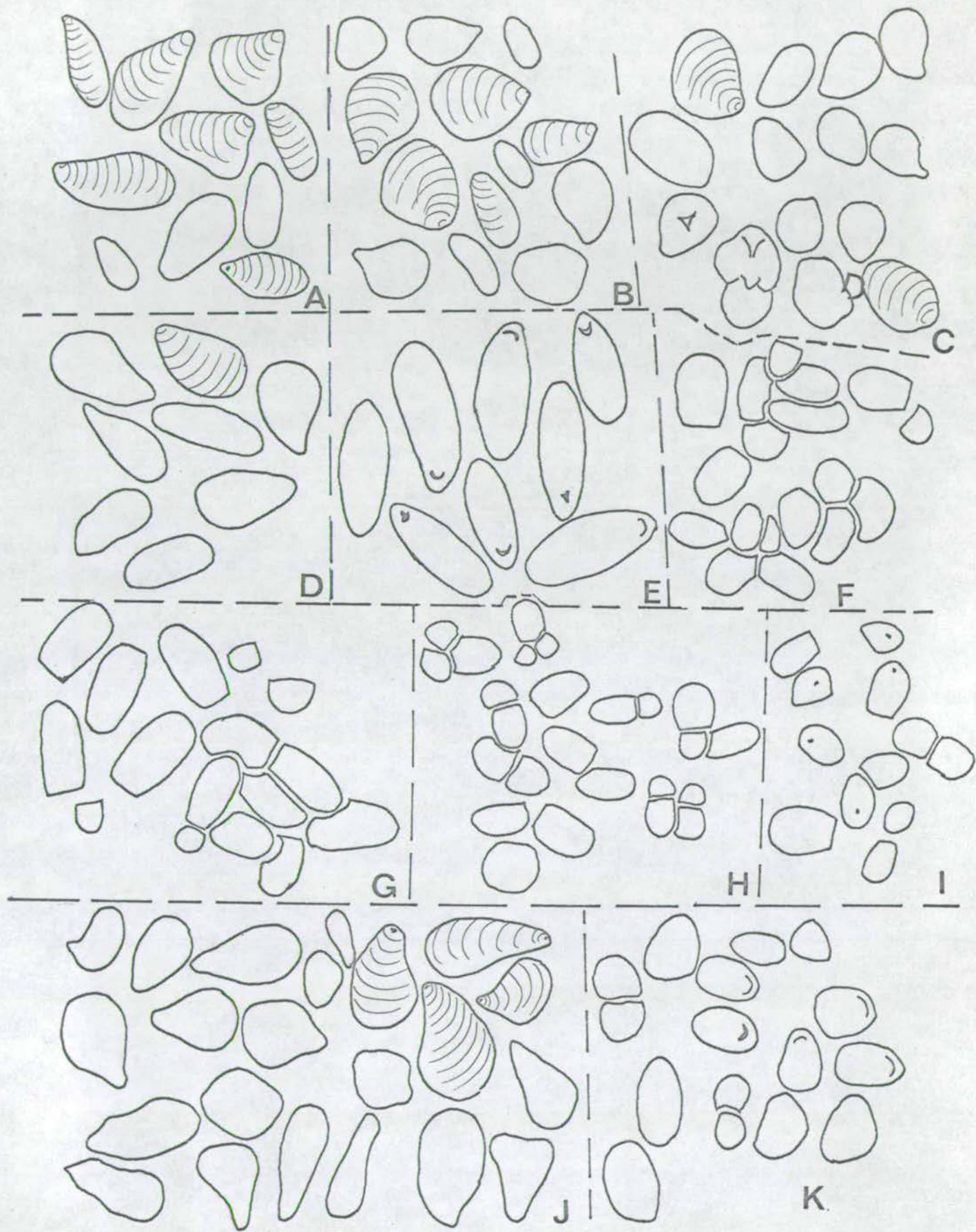


Fig. 27

tubers of the plants in this family. Sometimes, starch grains may be less abundant or absent as in Kaempferia rotunda and Roscoea purpurea. In these species and their allies, the reason is not usually far to find. The rhizomes are short (see page 14), rarely swollen to store food, but the root tubers essentially become the storage organs in which starch grains are abundant. Transitional starch grains may be numerous in the mesophyll cells of the lamina (according to Tomlinson 1956), but most of these are yet less mature than those in the rhizomes. From the leaf, there is a gradual decrease in the abundance of the starch grains to the sheath and stem. The starch deposits are occasionally found around the vascular elements in the cortex of the sheath where they are associated with the bundles. In the rhizome, starch is commonly found between the endodermis and the outer cortex and may be found in the central cylinder as in Zingiber officinale. In the root, starch is common in the storage tubers where they may occupy the cortex and pith, as in Roscoea, Kaempferia and Curcuma.

VASCULAR ELEMENTS

(1) Xylem elements.

The tracheal elements were studied from the materials of about fifty species belonging to different genera of the family. The methods employed for the preparation of the tracheal elements have been described on page 8. The observations made are summarised below:

Tracheids are present in all the parts of the plants, from the root to the lamina. The tracheids in the leaf sheath and lamina are usually very long and consist of numerous helically wound or scalariform bands (fig. 28.A). Angular tracheids and those with circular outline were observed in most of the lamina, particularly the latter is more frequent in the species of Zingiber

and Alpinieae.

The end walls where the adjacent tracheids overlap are imperforate, very long and oblique. Tracheids which were very similar to vessel-tracheids were observed in the roots and rhizomes of most plants particularly in the tribes Hedychieae and Globbeae. These tracheids are long with tapering oblique end plate which may be scalariformly pitted (fig. 28.B). Whereas more specialised tracheids and vessel-tracheids with shorter end plate and conspicuous scalariform pittings were more frequent in the species of the Alpinieae.

VESSELS: Vessels were observed much more frequently in the roots than in the stem of all the species examined. Vessels at the different levels of specialisation were observed in the same specimens and the highest level of specialisation observed was taken as the culmination of specialisation within such organs. In the Globbeae and Hedychieae, many intermediate stages, between the vessel-tracheids, primitive vessel elements and some slightly advanced elements such as those with oblique end plate (where the end plate is not more than 2-3 times the diameter of the element) and numerous scalariform bars (fig. 28.C), were observed as the predominant condition in these tribes. Whereas slightly more advanced vessel elements were seen in the roots and at the base of the stem in Zingiber and Burbridgea pubescens. The vessel elements in these genera are shorter, with slightly oblique end plate whose length is less than twice the diameter of the element, and the scalariform bars are reduced greatly in number (fig. 28.D,E). Occasionally, very closely similar vessel elements, although fewer than in the above genera may be observed in the mature roots of Hedychium, e.g. H. greenii. In the roots of all the species of the tribe Alpinieae examined, it appears that more

specialised vessel elements are more frequent than in any of the species of the other tribes in the family. These elements have slightly oblique to transverse end plates, (fig. 28.F-H), the number of perforation bars is greatly reduced to few, between 3 and 1 or none in some cases. The perforation plate varies from scalariform (with fewer bars), to simple (without bars).

Similar gradations in the specialisation, as in the end plate, could be observed on the thickenings and pittings to the lateral walls of the vessel elements. These vary from the helical or scalariform walls on the tracheids to the reticulate and thin-walled pittings on some vessel-tracheids and less specialised vessel elements. There is also progressive increase in the thickenings of the different forms of vessel elements depending on how specialised such elements are. The most specialised elements have greatly thickened walls and the pittings are alternate.

The observations made in this study support the generalisations made by Cheadle (1953) concerning the phylogeny of the tracheids and vessels in the monocotyledons. Accepting Cheadle's conclusions on the evolution of the vessel elements, the most primitive vessel elements were observed in the roots of most species in the tribes Hedychieae, (e.g. Boesenbergia, Kaempferia and Curcuma) and Globbeae, where the vessel elements seem to be at similar level of specialisation or probably slightly more advanced in Hedychium which belongs to the former tribe. The vessel elements of the Zingibereae (Zingiber) appear to be more advanced than any of the species in the tribe Hedychieae except Burbridgea, whose elements are very closely similar, in specialisation, to those of Zingiber. The tribe Alpinieae, particularly the species of Alpinia, Amomum, Hornstedtia, shows the greatest abundance of more specialised vessel elements up to the highest level of specialisation that

FIG. 28. TRACHEAL ELEMENTS.

Explanation in the text.

- A. Boesenbergia sp. (B & M 5164)
- B. Globba aurantiaca.
- C. Hedychium greenii.
- D. Zingiber officinale.
- E. Burbridgea pubescens.
- F. Anomum cardamomum.
- G. A. cardamomum.
- H. Hornstedtia leonurus.

All figures x 340

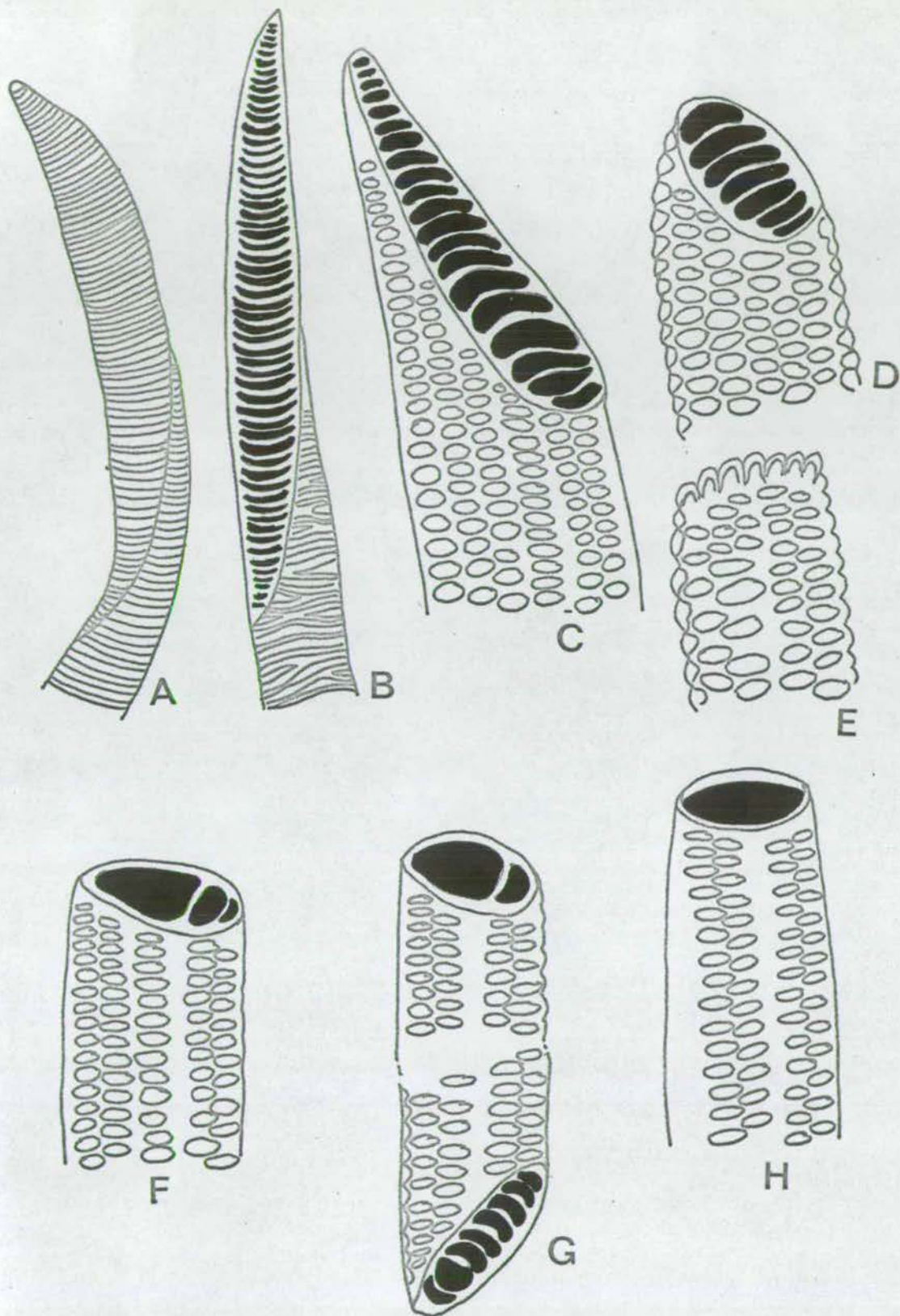


Fig. 28

could be found in the highly specialised families of the monocotyledons, such as the Gramineae. The conclusion that could arise from the preponderance of these highly specialised vessel elements in the tribe Alpinieae is that this tribe might be more advanced than any other in the family in regard to the evolution of the tracheal elements. Furthermore, because primitive vessel elements were more frequent in many species of the tribe Hedychieae than anywhere else, this tribe might contain the most primitive species or genera in the family. Moreover, because vessels are more or less restricted to the roots and fewer in the other parts of the plants (i.e. stem and leaves), the family is primitive in this respect.

(ii) PHLOEM ELEMENTS.

After the preliminary investigation on the phloem elements, the observations made were found to be similar to those reported for the family by Tomlinson (1956). Since, according to him, there is great uniformity in the structure and characteristics of the phloem elements throughout the family, further amplification on this was thought to be unnecessary. However, the sclerotic phloem parenchyma cells in Hornstedtia have been discussed on page 181.

The taxonomic value and phylogenetic significance of the tracheal elements are discussed on page 196.

IV. STOMATAL STRUCTURE AND ONTOGENYINTRODUCTION.

The structure of the stomata in the Zingiberaceae was described previously by Solereder and Meyer (1930), and recently by Stebbins and Khush (1961) and Tomlinson (1956, 1969). Stebbins and Khush, in their extensive work on the structure and development of stomata in the monocotyledons, grouped the Zingiberaceae in the first category of stomata types, i.e. those with two guard cells and four to six subsidiary cells. In this category were also such families like the Strelitziaceae, Musaceae, Cannaceae, Araceae, Commelinaceae and Bromelliaceae. These workers, however, reported two lateral subsidiary cells for two unidentified species; Amomum sp. and Zingiber sp. Furthermore, Tomlinson (1956) reported that the stomata in this family are tetracytic but in his recent work, he grouped the family with those whose stomata are paracytic (Tomlinson 1969, page 404).

From the above reports, it seems that the dependence on the mature stomatal complex for the interpretation of the type of stomata, and number of subsidiary cells without the study of the developmental relationships, might lead to erroneous results. This is probably because the cellular alignments in the mature epidermis, often conceal the developmental relationships between subsidiary cells and their precursors. This reason certainly applies to the family Zingiberaceae. Apart from the work of Stebbins and Khush, where they related the stomatal development in the Zingiberaceae to that of Tradescantia (Comelinaceae), there has been no report on the study of stomatal ontogeny in this family. Also, such studies are much needed in the remaining seven families of the order Zingiberales.

TERMINOLOGY.

Some of the common terminologies, on the types of stomata in the monocotyledons, i.e. those of Metcalfe (1960) and Pant (1965), were adopted in this study. Stoma (pl. stomata) refers to both guard cells and surrounding cells which together have been organised in a recognisable pattern.

The protodermal cells (meristemoid) which divide to produce the guard cells, is termed guard cell mother cell, heretoeafter referred to as g.c.m.c. The g.c.m.c. and the surrounding cells were produced by the divisions of protodermal cells, such cells are termed meristemoids. Protodermal cells are the products of the apical meristem. A meristemoid which divides to produce a subsidiary cell is referred to here as the subsidiary cell initial (s.c.i.). If it is lateral or terminal in position, it is termed lateral (l.s.c.i.) or polar (p.s.c.i.) subsidiary cell initial respectively. When the subsidiary cells are produced by the divisions of the cells surrounding the g.c.m.c. such development is termed perigenous and the initials are termed perigenes. Paracytic stomata - stomata with two distinct lateral subsidiary cells, one on either side of, and parallel to, the guard cells. Tricytic stomata - stomata with two lateral and one polar subsidiary cells. Tetracytic stomata - stomata with two lateral and two terminal subsidiary cells, one on each of the four sides, as seen in surface view. Polycytic stomata (Pant and Benerji 1965), with more than four subsidiary cells (i.e. may be 5-8 cells) around the guard cells.

MATERIALS AND METHODS

For the mature stomata, the epidermis of the lamina of all the cultivated and herbarium materials for about ^{three} hundred and ~~five~~ species which came under this study, were examined (see appendix for list of species). The

stomata development was studied from the cultivated specimens of about thirty-six species. The materials were taken among those cultivated in the glass houses at the Royal Botanic Gardens, Edinburgh. The species marked (S) in the appendix were those whose stomata developments have been investigated.

Young developing plants were collected and the young leaves which were rolled inside the concentric layers of leaf-sheaths, were dissected out by slashing the stem into longitudinal halves. The bit of the young leaves were fixed in 3:1 alcohol-acetic mixture for at least one hour. It is usually difficult to peel off the epidermis from the young leaves at this stage because they are delicate and brittle. Small portions of about 5 mm. x 2 mm. were cut off at regular intervals from the youngest part in the base of the leaf to some distance up it where the leaf is more mature. Growth of the leaf, as in other monocotyledons, is basipetal and the different stages of stomata development could be found on the same leaf, but at different levels along it. The small portions were mounted whole in 1% acetocarmine on slides. The slides were warmed over a hot plate until boiling. When cooled, they were sealed off with Dunlop rubber solution. The slides were all temporary preparations and they remain good for about two to five days, but according to Stebbins and Khush (1961), such slides, if kept in the refrigerator, remain good for several weeks. The nuclei stained almost within five minutes and could be studied immediately, but for photomicrographs, the nuclei become deeply stained after about six hours (Stebbins and Khush 1961). Camera lucida drawings and photographs of the developmental stages were made from the slides.

For the mature stomata, portions of the mature leaves were taken from the standard median level and fixed in formol-acetic-alcohol solution. Dried

herbarium materials were boiled in water containing one pellet of potassium hydroxide for about ten to fifteen minutes. The addition of the KOH enables the epidermis to separate very easily. The epidermal peels of both the adaxial and abaxial surfaces were washed severally in water, where the peels are coloured as with the herbarium specimens, the peels were bleached in about 25% of domestic peroxide, and then washed in many changes of water. Both the epidermal peels from green plants and herbarium specimens were stained in 10% Delafield's haematoxylin for about 10-15 minutes, washed in water to remove excess stain and then differentiated in 50% alcohol to which a few drips of conc. HCl was added. The peels were again washed in water many times, taken through the grades of alcohol up to 95% and mounted in euparal. Some temporary epidermal preparations were stained in 1% safranin in 50% absolute alcohol and mounted in diluted glycerine solution. Such preparations keep for many months. Camera lucida drawings of the mature epidermal cells and stomata were made and the stomatal developments were photographed.

Measurements of the guard cells were made during the preliminary study, but these show that the size of the guard cells varies in the different species and the range of size for the genera appear to be uniform throughout the family. These measurements were thought to be of less significance for the generic determinations and have, therefore, been excluded from detailed consideration, although the range of the sizes of the guard cells will be found in the descriptions for the genera.

The stomatal index and relative frequency of the different stomata types were investigated for thirty-two species. The results of this investigation are listed in Table 4. The stomatal index (S.I) is the percentage of the total number of cells present per sq. mm. of the epidermis,

i.e.

$$\frac{\text{number of stomata}}{\text{total no. of epidermal cells (including the stomata)}} \times \frac{100}{1} = S.I$$

OBSERVATIONS.

The leaves are amphistomatic in all the species examined, although the stomata are more frequent on the abaxial than the adaxial epidermis. The stomata were found more commonly in the intercostal areas on both surfaces, except in some few genera or species, e.g. Scaphochlamys (fig. 11.f) and to some extent in Renealmia, where the abaxial epidermis is almost uniform, i.e. the costal cells were not obviously modified in a different way to the adjacent intercostal cells. Stomata were found in the epidermis of the sheath, ligule, and floral bracts.

Guard cells are often flush with the epidermal surface but the subsidiary cells may be slightly sunken (fig. 29.a,b). The stomata of Boesenbergia sp. (B 4927), are elevated on top of mounds which appear as turrets on the abaxial epidermis (fig. 29.c). The guard cells may be slightly asymmetric, and the inner and outer ledges are frequently thickened. The orientation of the guard cells is unidirectional and parallel to the long axis of the lamina. Cuticular striations (fig. 29.d,e) were observed more frequently in the Alpinieae. These striations are more prominent in the lateral subsidiary cells than in any other cells except in Zingiber puberulum, where they are conspicuous in other cells (fig. 29.d).

The mature stomata in all these plants belong to four types, i.e. paracytic (fig. 30.a,b), tricytic (fig. 30.f; Plate 7.b), tetracytic (fig. 30.c,d; Plate 7.a,e,f) and polycytic (4-8 subsidiary cells) (fig. 30.d,e; Plate 7.c,d). The tetracytic stomata is by far the most predominant and the relative frequency may reach up to 95% of the total stomata in most genera (Table III). The

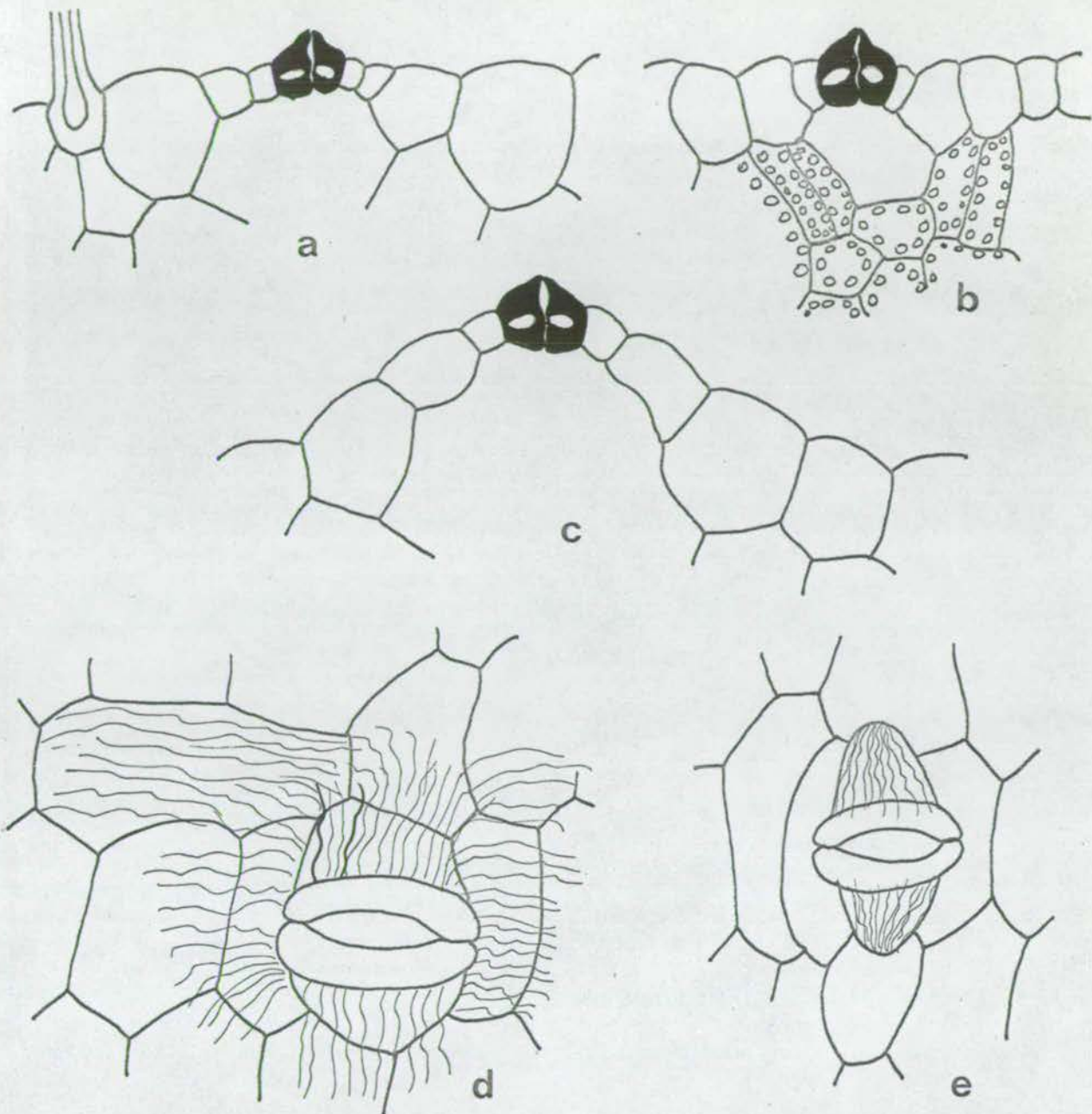


Fig.29

**FIG. 29. STOMATA IN TRANSVERSE SECTION
AND CUTICULAR STRIATIONS.**

Explanation in the text.

- (a) Camptandra Latifolia.
- (b) Zingiber officinale.
- (c) Boesenbergia sp. (B4927).
- (d) Zingiber puberulum.
- (e) Renealmia exaltata.

Figures a - c x 340; d,e. x 680.

TABLE 4. STOMATAL INDEX AND RELATIVE FREQUENCY OF THE DIFFERENT TYPES OF STOMATA.

SPECIES	Average total number of Epidermal cells and Stomata per mm ² .						$\left(\frac{B}{A} \times \frac{100}{1} \right)$ STOMATAL INDEX	PERCENTAGE RELATIVE FREQUENCY OF:-			
	A	B	C	D	E	F		PARACYTIC STOMATA	TRICYTIC	TETRACYTIC	POLYCYTIC
	EPIDERMAL CELLS (+B)	STOMATA	PARACYTIC STOMATA	TRICYTIC	TETRACYTIC	POLYCYTIC					
1. Globba atrosanguinea	98	6	.5	.3	4	1	6.12	8.3	5	66.6	16.6
2. Mantisia wardii	93	7	-	-	6	1	7.52	-	-	85.7	14.2
3. Roscoeia cautleoides	50	6	-	-	5	1	12.0	-	-	83.3	16.6
4. R.purpurea	96	10	1.0	1.0	7	1	10.4	10.0	-	70.0	10.0
5. Cautleya robusta	107	13	-	-	11	2	12.1	-	-	84.6	15.3
6. Boesenbergia sp. (B&M. 5164)	49	3	-	-	1	2	6.3	-	-	33.3	66.6
7. B.hutchinsonii	82	4	-	-	2	2	4.8	-	-	50.	50.0
8. B.parvula	25	2	-	-	-	2	8.0	-	-	-	100.0
9. B.sp.(B.4927)	23	4	-	-	1	3	13.04	-	-	25.0	75.0
10. B.plicata	29	4	-	-	1	3	10.3	-	-	25.0	75.0
11. B.sp. (B.4706)	41	4	-	-	2	2	10.0	-	-	50.0	50.0
12. Kaempferia rotunda	40	4	1.0	-	2	1	10.0	25.0	-	50.0	25.0
13. K.pulchra	62	4	.2	-	2	2	6.4	-	-	50.0	50.0
14. K.gilbertii	38	4	-	-	3	1	10.5	-	-	75.0	25.0
15. K.elegans	44	4	-	-	1	3	8.8	-	-	25.0	75.0
16. Caulokaempferia coenobialis	44	3	-	-	3	-	6.8	-	-	100.0	-
17. Scaphochlamys klossii	112	6	-	-	3	3	5.36	-	-	50.0	50.0
18. Burbidgea pubescens	45	5	-	-	4	1	11.1	-	-	80.0	20.0
19. B.sp. (B&W 5314)	48	4	-	-	3	1	8.3	-	-	75.0	25.0
20. Camptandra latifolia	28	3	-	-	2	1	10.6	-	-	66.6	33.3
21. Brachychilum horsfieldii	142	8	-	-	6	2	5.7	-	-	75.0	25.0
22. Zingiber officinale	112	11	-	-	10	1	9.7	-	-	90.9	9.09
23. Z.mollis	126	8	-	-	7	1	6.3	-	-	87.5	12.5
24. Hedychium forrestii	97	7	-	-	6	1	8.86	-	-	85.7	14.2
25. Riedelia sp. (Millar 14594)	96	10	-	-	9	1	10.1	-	-	90.0	10.0
26. Hornstedtia villosa	229	20	-	-	19	1	8.7	-	-	95.0	5.0
27. Elettaria surculosa	201	11	-	-	10	1	5.5	-	-	90.9	9.09
28. Cenolophon sp.(B2268)	102	8	2.0	3.0	3	-	7.84	25.0	37.5	37.5	-
29. Alpinia allughas	397	15	-	-	13	2	3.7	-	-	86.6	13.3
30. A.galanga	192	12	1.0	1.0	9	1	6.2	8.3	8.3	75.0	8.3
31. A.mutica	138	16	-	.2	15	1	11.6	-	-	93.8	6.25
32. Aframomum luteo-album	392	18	.5	.5	16	1	4.5	2.8	2.8	88.8	5.6

paracytic and tricytic types were encountered only occasionally (fig. 30.f), as in Cenolophon sp. (B 2268). There is much variation in the relative frequency of the polycytic stomata. In most genera, except Boesenbergia, and some species in Kaempferia and Camptandra, the frequency may never be more than 5%, whereas in the latter genera, it could reach up to between 45% and 70% of the total stomata on a lamina. Occasionally, as in Boesenbergia parvula (fig. 30.d), there may be an increase in the number of subsidiary cells, up to 8 and 10 around the guard cells.

It was observed that the tetracytic nature of the stomata complex were more easily recognisable in the tribes Globbeae (fig. 30.a), Hedychieae and Zingibereae (Zingiber) than in the Alpinieae (fig. 30.b). In all the tribes the lateral subsidiary cells are distinct in shape and size from the adjacent epidermal cells. Also in the Globbeae, Hedychieae and Zingibereae, the polar subsidiary cells are distinct, in their narrower dimension, from the adjacent wider epidermal cells. But in the Alpinieae, it appears that the polar subsidiary cells are much less distinct from the epidermal cells. All these cells are narrow and strongly elongated transversely that any investigator examining the mature epidermis alone might take the stomatal complex as paracytic. In this tribe, the true relationships of the polar subsidiary cells is concealed in the mature stomata and the study of the developmental processes yielded evidence to support their subsidiary nature (page 157).

The observations made on the types of stomata in this study support the category under which Stebbins and Khush (1961) grouped the Zingiberaceae. But the tetracytic nature of all the stomata in the family disagrees with their observation on Amomum sp. and Zingiber sp.

ANOMALOUS STOMATA

Various kinds of abnormal stomata were observed in most of the species. Stomata with multiple subsidiary cells are frequent in Boesenbergia parvula (fig. 30.d; Plate 7.d). Although, it is true as was described above, that the stomata in this genus are polycytic, some of the subsidiary cells were produced in a rather abnormal manner, particularly the polar cells. Apart from the 6-8 normal subsidiary cells around the guard cells, some of the polar cells contain two to three horizontal or oblique thin-walled partitions in them. Such partitions are believed to have been produced as a result of further divisions in these cells. This type of horizontal or oblique divisions in the subsidiary cells is uncommon in the family.

Contiguous stomata (fig. 31.a,c,e-h,l,o; Plate 7.e,f) are particularly frequent in Globba and the genera of Alpinieae. Some of the contiguous stomata may be superimposed, (fig. 31.e; Plate 7.e,f) or they may be in contact only through their subsidiary cells (fig. 31.c,f,l). Some stomata have two or three lateral subsidiary cells on one side as in Boesenbergia sp. (B & M 5164) (fig. 31.a), while others share their subsidiary cells as in B. sp. (Woods 1549) (fig. 31.c), Globba atrosanguinea (fig. 31, e,f), and Alpinia allughas (fig. 31.c). In some stomata, one lateral subsidiary cell may be shared by two guard cells (fig. 31.g), or the lateral subsidiary cell of one may become the polar cell of the other (fig. 31.c). Series of many superimposed stomata are frequent in the tribe Alpinieae and Cautleya robusta (fig. 31.l). In these groups, many stomata share successive subsidiary cells and in most cases, the normal pattern of cells around the guard cells is disrupted. Other abnormal stomata encountered include malformed guard cells with one cell developed as in Burbidgea pubescens (fig. 31.i), or where the

FIG. 30. TYPES OF MATURE STOMATA.

- a. Globba atrosanguinea - tetracytic stomata.
- b. Elettaria surculosa - tetracytic stomata.
- c. Boesenbergia hutchinsonii - polycytic stomata.
- d. B. parvula - polycytic stomata.
- e. Kaempferia elegans - tetracytic and polycytic stomata.
- f. Cenolophon sp. (B 2268) - paracytic, tricytic and tetracytic stomata.

All figures x c.180

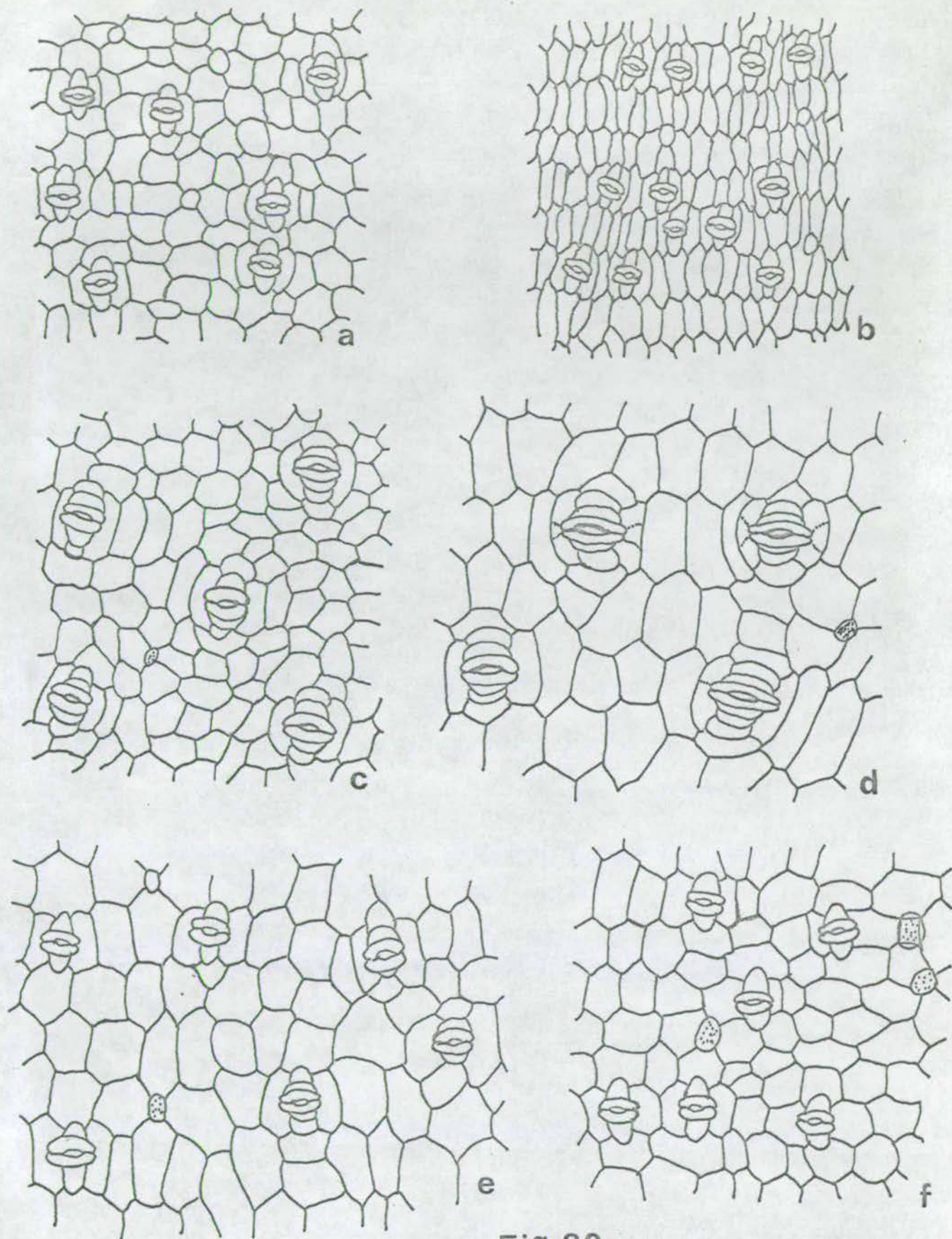


Fig. 30

FIG. 31. ABNORMAL STOMATA.

Explanation in the text.

- | | |
|--|--|
| a. <u>Boesenbergia parvula.</u> | b. <u>Boesenbergia sp.</u>
(B & M 5164) |
| c. <u>B. sp. ?</u> (Woods 1549) | d. <u>Rhynchanthus beesianus.</u> |
| e, f. <u>Globba atrosanguinea.</u> | g. <u>Cautleya robusta.</u> |
| h. <u>Kaempferia elegans.</u> | i. <u>Burbidgea pubescens.</u> |
| j. <u>K. rotunda.</u> | k. <u>Kaempferia rotunda.</u> |
| l. <u>Cautleya robusta.</u> | m. <u>Burbidgea pubescens.</u> |
| n. <u>Burbidgea pubescens.</u> | o. <u>Alpinia allughas.</u> |
| p. <u>Boesenbergia sp. ?</u> (Woods 1549). | |

figures a - m, and p. x 180; n, o. x 680.

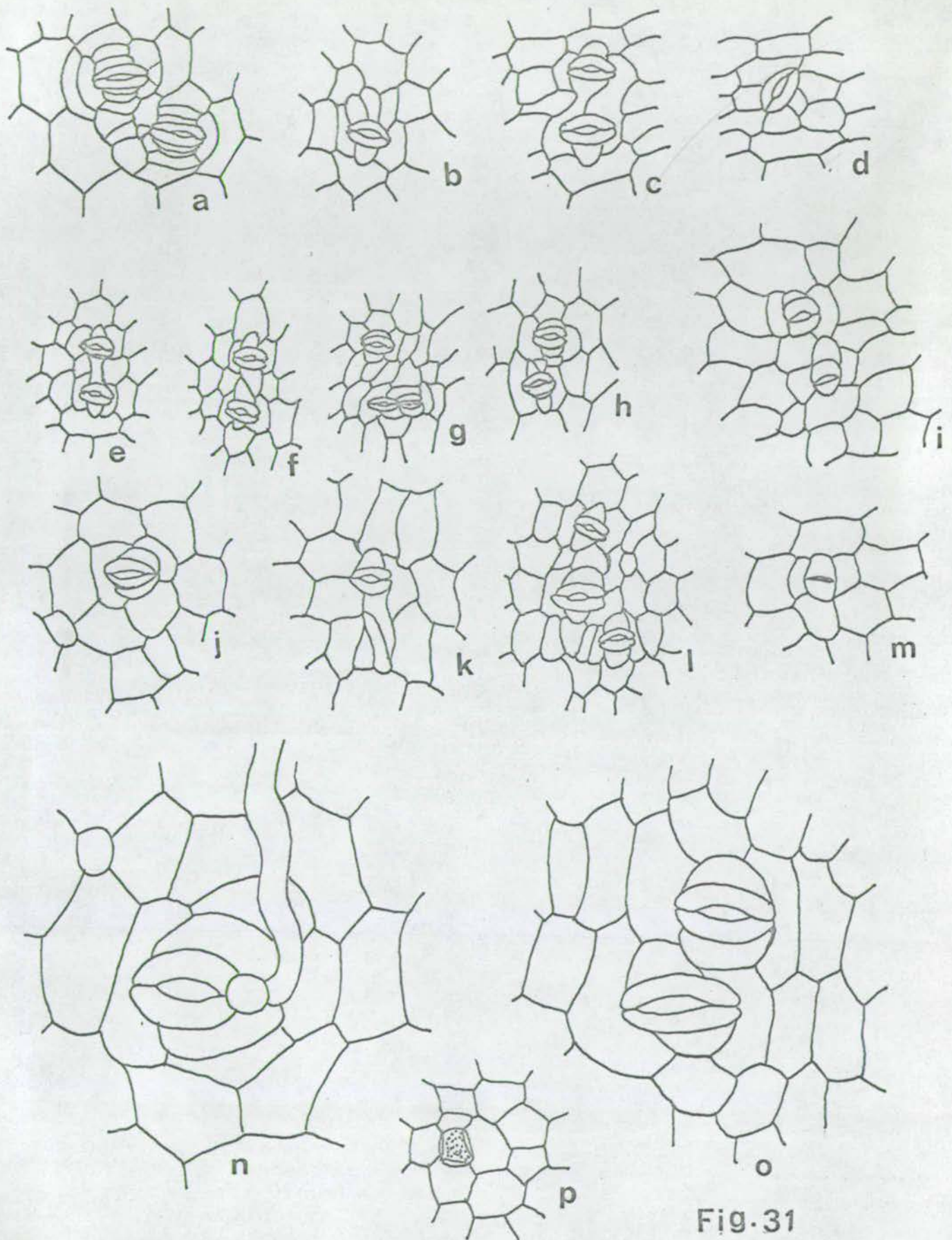


Fig. 31

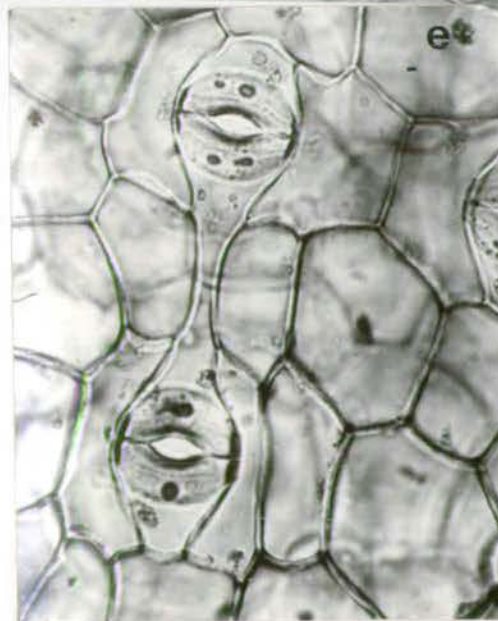
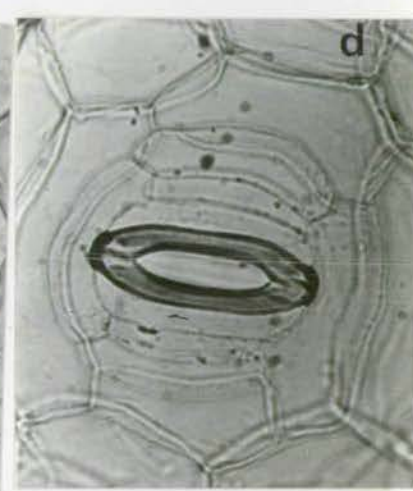
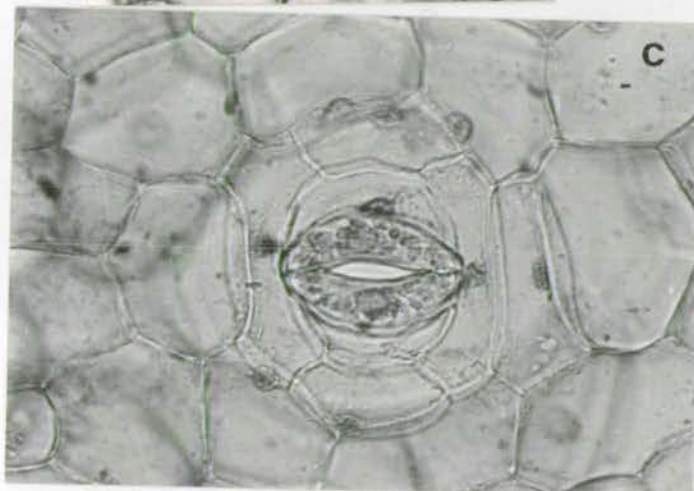
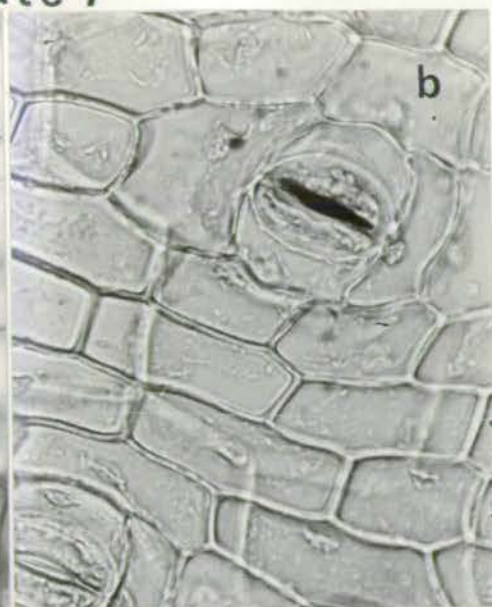
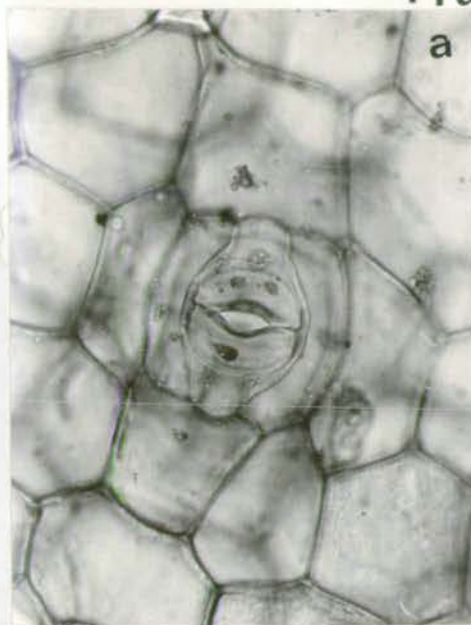
PLATE 7. MATURE AND ABNORMAL STOMATA.

Explanation in the text.

- a. Globba atrosanguinea.
- b. Boesenbergia sp.? (Woods 1549).
- c. Boesenbergia sp. (B 7 M 5164)
- d. B. parvula.
- e, f. Globba atrosanguinea.

Figures a,c-f x c.450; b. x c.580

Plate 7



stomal pore failed to open (aborted guard cell) (fig. 31.m). Some stomata may have the subsidiary cells arranged in an almost cyclocytic pattern as in Kaempferia rotunda (fig. 31.j), and others may be normal but with vertical division in the polar cells (fig. 31.k). In K. rotunda, it was also observed that there may be some indication of meristematic struggle between two potential lateral perigenes (fig. 31.k). In this example, the two close cells to the guard cells divide variously but one managed to contribute its product to the guard cells as the lateral cell. Occasionally, some stomata are contiguous with either hair bases or oil cells as in Burbridgea pubescens (fig. 31.n). Furthermore, some oil cells or hair bases were found with either one or two smaller subsidiary-like cells (fig. 31.p), as in Boesenbergia sp. (Woods 1549). This kind of abnormal subsidiary-like cell is probably of some importance in the discussion of the mechanisms that may be responsible for the divisions of the perigenes around the guard cell mother cells.

STOMATAL DEVELOPMENT.

TETRACYTIC STOMATA (fig. 32.a-f; Plate 8.a-g).

The development of the stomata is perigenous in all the species examined. The guard cell mother cell (g.c.m.c.) arose among the longitudinal rows of protodermal cells which have, in turn, been derived from the apical meristem. The development of these cells is basipetal, i.e. the youngest part is found at the base of the developing leaf. The different stages are located at certain intervals from the base upwards, through the length of the leaf until there are mature stomata.

At the earlier stage, very close to the base of the leaf, all the protodermal cells appear similar (Plate 8.a,b). It is common to find some of

the protodermal cells at this stage still dividing, particularly with the walls perpendicular to the long axis of the lamina except on the veins, where the cells may also divide longitudinally and asymmetrically (Plate 8). Many of the protodermal cells which divide vertically produce cells (meristemoids) which are narrow at first, but rapidly become large and more or less isodiametric or rectangular (fig. 32.a; Plate 8.a). These cells are variously interspersed among the other protodermal cells and they become either the guard cell mother cells, or cells which differentiate without further divisions into oil cells or indumentum (Plate 8.b). At some distance from the base of the leaf, when the guard cell mother cells become distinguishable, all the protodermal cells are potentially meristematic, but few of them may be found dividing beyond this stage in the Globbeae, Hedychieae, and Zingibereae. In most species of the tribe Alpinieae, e.g. Aframomum luteo-album (B4634), (Plate 8.), and Alpinia mutica, the protodermal cells continued for a much longer time, dividing rapidly and producing both new protodermal cells and meristemoids. These divisions continue even further when mature stomata are present (Plate 8.g), and some of the epidermal cells have differentiated. After this stage, the divisions and production of new cells gradually ceases. More of the youngest stomata produced by the new meristemoids are frequently observed among the mature stomata (Plate 8.g). This more prolonged meristematic activity of the protodermal cells before and at times beyond the stage where the guard cell mother cells divide and mature has some bearings on the cellular alignment in the mature epidermis of the Alpinieae (see page 169).

The guard cell mother cells differentiate very rapidly from among the other protodermal cells and are distinguishable by their large size, copious cytoplasm, dense and deeply staining nuclei, rounded corners and their

refringence under the light microscope (Plate 8.a-d). Also, at this stage, the oil cells and hair initials show some similarities to the g.c.m.c. from which they could not be easily separable. But the oil cell initials rapidly differentiate to contain some oil globules; the hair initials also differentiate and the apical elongation appears first as papillae (Plate 8.b). This is followed by rapid elongation and vacuolation of the cell walls and cytoplasm respectively.

The four protodermal cells surrounding the g.c.m.c. belong to three adjacent parallel rows, viz. the upper lateral subsidiary cell mother cell in the upper row to that in which the g.c.m.c. is in, the lower lateral subsidiary cell initial (l.s.c.i.) in the lower row to the g.c.m.c. and two polar cells, one on either side of the g.c.m.c. in the same row as the latter (fig. 33. A, D, E). These subsidiary cell initial (s.c.i.) and likewise the g.c.m.c. are products of the asymmetric divisions of the protodermal cells (meristemoids). These subsidiary cell initials are also easily distinguishable by their deep-staining nuclei which are also drawn close to the intervening walls between them and the g.c.m.c. Sometimes, the oil cell and hair initials may be surrounded by similar cells as if they would produce subsidiary cells. Of course, some do very rarely, as observed in Boesenbergia (Woods 1549) where the mature oil cells have a small subsidiary cell close to it. Also, a subsidiary cell close to the base of a simple hair has been observed in Aframomum luteo-album (B 4634).

Usually the lateral subsidiary cell initial divides first and asymmetrically with the wall laid down obliquely or parallel to the lamina axis; to produce two cells. One of these cells is smaller and close to the g.c.m.c., while the other may be larger and separated from the g.c.m.c. by the

smaller cell (fig. 32.b,c; Plate 8.c-f). Then the polar subsidiary cell initials divide, the separating wall being at right angles to the horizontal, to produce the two polar subsidiary cells, one on either side of the g.c.m.c. (fig. 32.a-d; Plate 8.d-f). There is no general synchronisation in which the subsidiary cell initials divide first, but the only constant pattern observed is that the g.c.m.c. divides after the subsidiary cell initials round it have done so, or are in the process of division. But where the polar subsidiary cell initials do not divide, or only one divides, as in some stomata in Cenolophon sp. (B 2268), the g.c.m.c. divides probably as a result of the increasing differentiation of the epidermal cells around it or after a period of time. The result of such activities is that, where the two polar subsidiary cell initials do not divide, only two lateral subsidiary cells are present around the guard cells, hence some stomata are paracytic on the lamina of this species (fig. 30.f; 33.B.C). Where one of the polar subsidiary cell initials divides, two lateral and one polar subsidiary cells were found (fig. 30.f; 33.B.C). But where both the two lateral and two polar subsidiary cell initials divide in the normal way, tetracytic stomata are produced, (fig. 30.a,f).

The guard cell mother cell divides (fig. 32.d,e; Plate 8.f) only once and a crescentric pore is formed in between two daughter cells to produce the two guard cells. The stomatal opening is always parallel to the long axis of the lamina except in abnormal cases, where it may be oblique (fig. 31.d).

POLYCYTIC STOMATA (fig. 32.g-n; Plate 9.a-i).

The presence of extra cells adjacent to the stomata is probably not due to an ordinary modification of the adjacent epidermal cells as was suggested by Tomlinson (1956), but these cells, subsidiary cells, were the products of

the multiple divisions of the subsidiary cell initials.

In the polycytic stomata (with 5-8 or more subsidiary cells) the stages are the same up to the complete divisions of the four subsidiary cell initials around the g.c.m.c. and before the latter divides. The first produced lateral subsidiary cell may divide again (fig. 32.i,j; Plate 9.e,f) or the remaining cell after the production of the first formed lateral cell may divide (fig. 32.i; 33.E-H). The products of the divisions of these two types of cell are added as narrow cells to the previous subsidiary cells and they become part of the stomatal complex (fig. 32.j-n; Plate 9.g-i). Occasionally, only one such first-formed subsidiary cell divides again to produce the second lateral subsidiary cell from one side to produce stomata with three lateral subsidiary cells; or where the two lateral subsidiary cells divide again, two smaller subsidiary cells are present on either side of the guard cells. Occasionally after the first division of the lateral subsidiary cell initial from one or both sides of the g.c.m.c. the remaining cell/cells may be small. Such cell/cells may become differentiate to appear as subsidiary cells (fig. 30.d; 32.l,n). This type of cells are very close to the modified epidermal cells suggested by Tomlinson (1956). Where only the products of the first division of the lateral subsidiary cell initials (i.e. the first formed subsidiary cells or the remaining subsidiary cell initial) divide, there may be 4-6 lateral subsidiary cells around the stomata as in Boesenbergia sp. (B & M 5164)(fig. 32.k-m). In Boesenbergia parvula there may be many more than two divisions of the lateral subsidiary cell initial or its earlier product and in such a case, and with occasional modification of the remaining cell into subsidiary-like cell, there may be up to six lateral subsidiary cells produced (fig. 30.d; 32.m,n; Plate 7.c,d). In Boesenbergia, the polar subsidiary cell initials

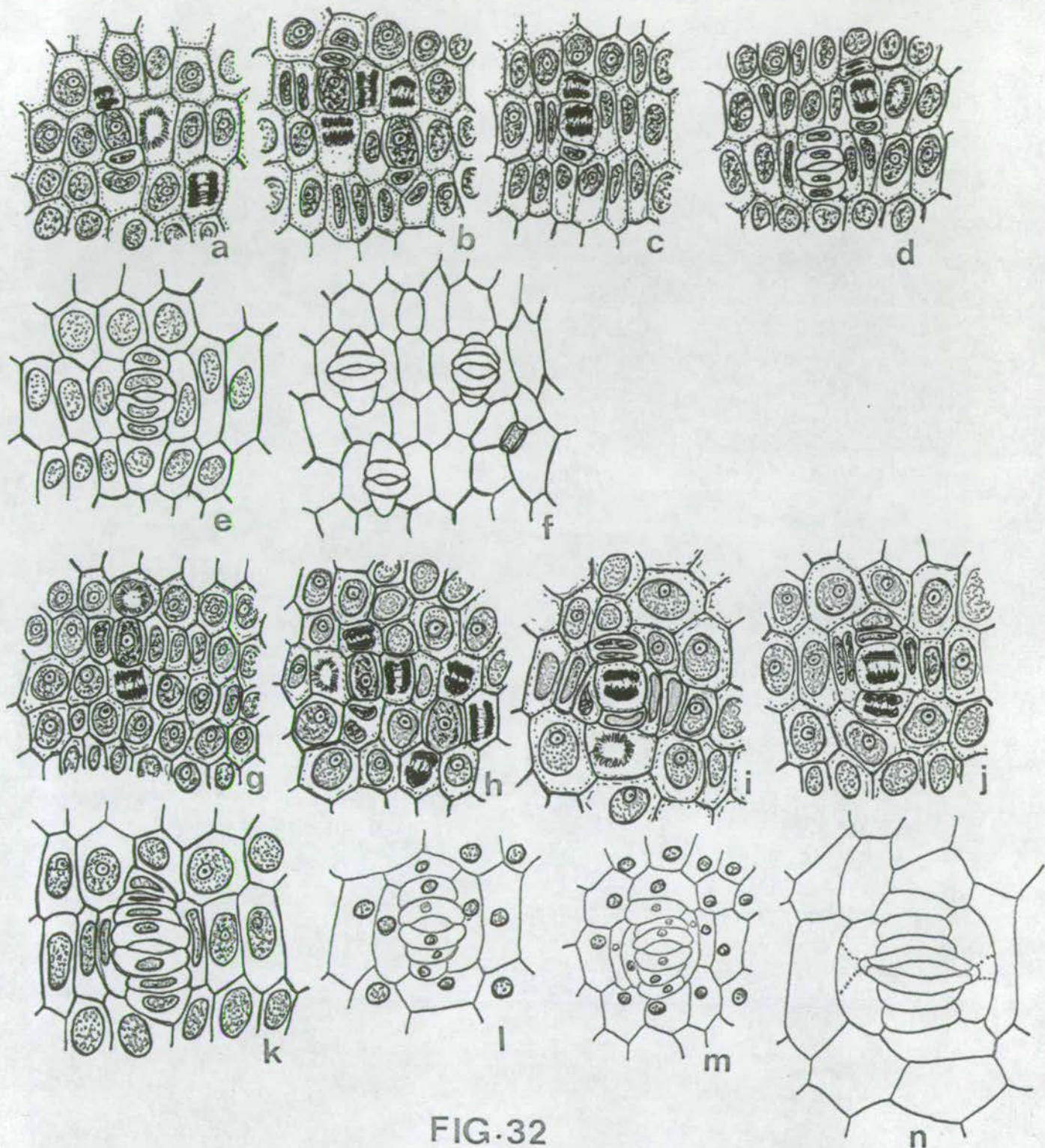


FIG. 32

FIG. 32. STAGES IN THE STOMATAL DEVELOPMENT.

Explanation in the text.

- (a - f) *Aframomum luteo-album*.
 (g - m) *Boesenbergia* sp. (B & M. 5164).
 (n) *B. parvula*.

Figures a-f x c.600; g-m x c.420; n x c.330

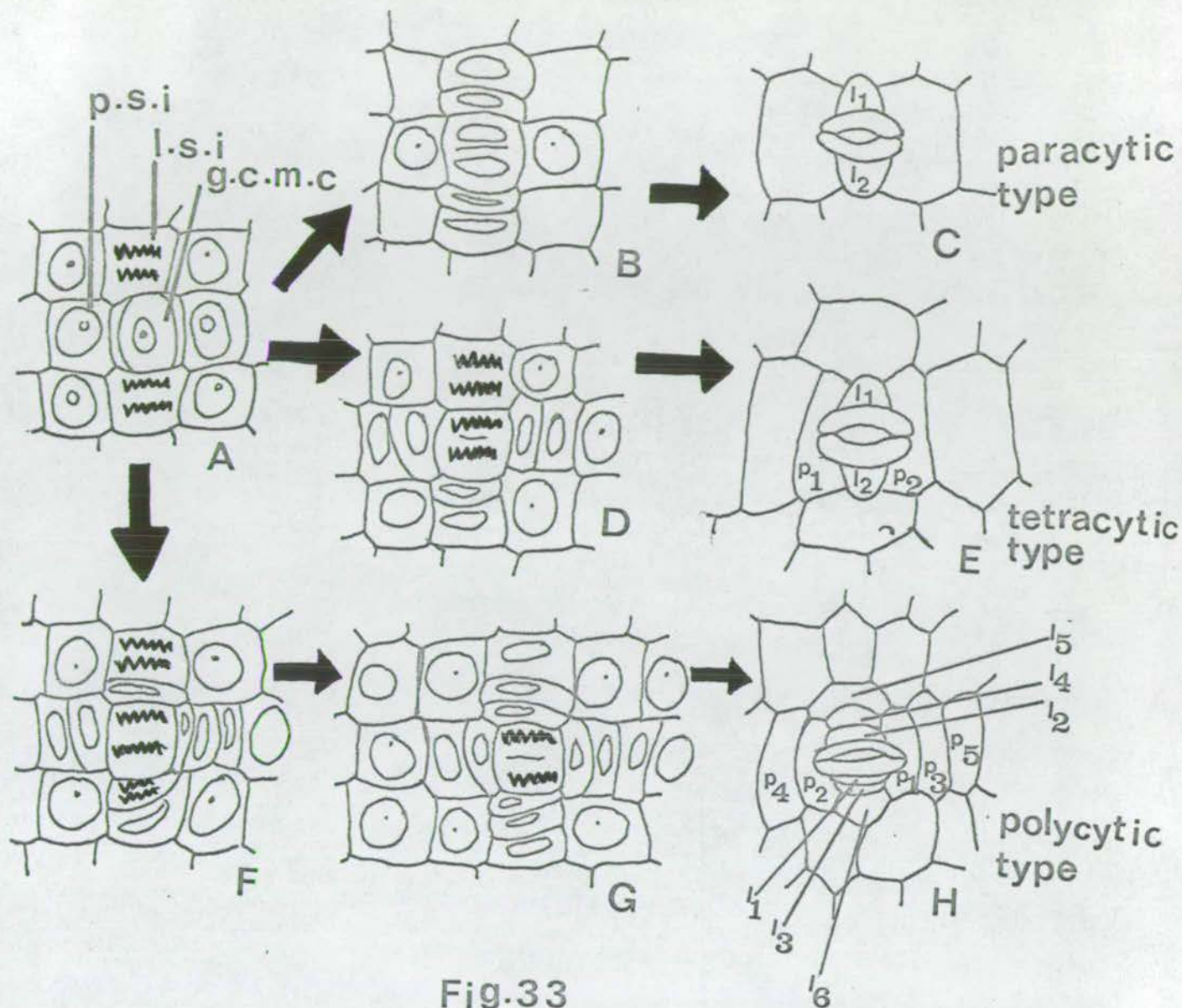


Fig.33

FIG. 33. SCHEMATIC REPRESENTATION OF THE DEVELOPMENT OF THE DIFFERENT STOMATAL TYPES.

(A) Guard cell mother cell (g.c.m.c) and the perigenes; (B-C) paracytic type; (D-E) tetracytic type; (F-H) polycytic type.

g.c.m.c. = guard cell mother cell.
 l.s.i = lateral subsidiary cell initial.
 p.s.i = polar subsidiary cell initial.
 l₁, l₂, l₃-l₆ = lateral subsidiary cells.
 p₁, p₂, p₃-p₅ = polar subsidiary cells.

PLATE 8. STAGES IN THE STOMATAL DEVELOPMENT - I.

Explanation in the text.

a. - g. Aframomum luteo-album

g.c.m.c. = guard cell mother cell; h = developing hair;
l.s.i. = lateral subsidiary initial; p.s.i. = polar
subsidiary initial.

Figures a & b x c.600; c-f x c.750; g x c.860

Plate 8

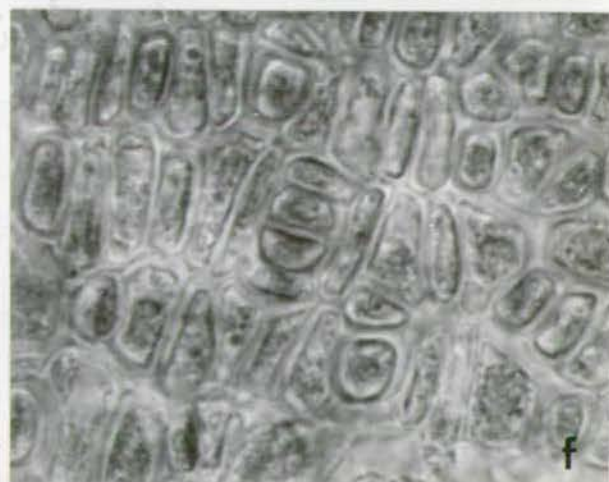
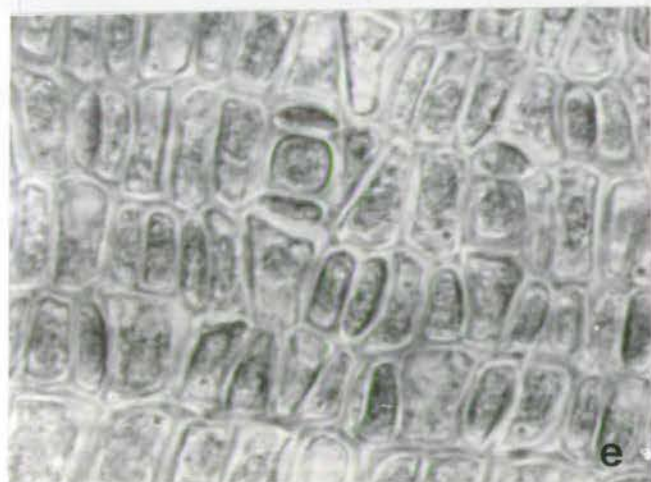
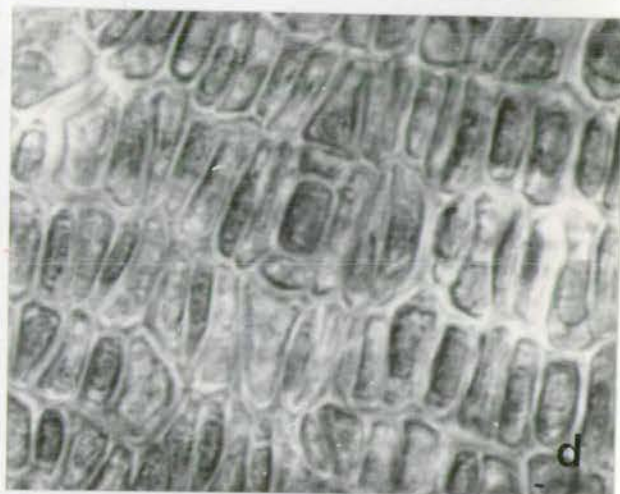
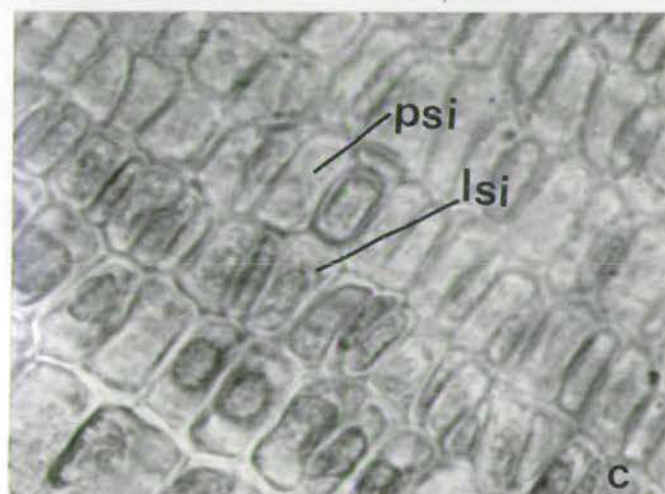
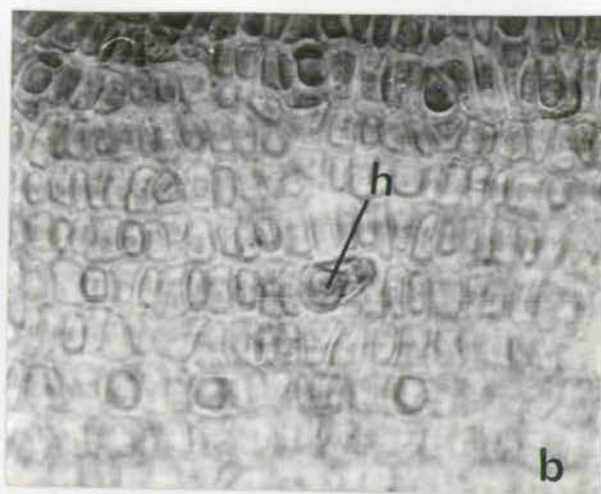
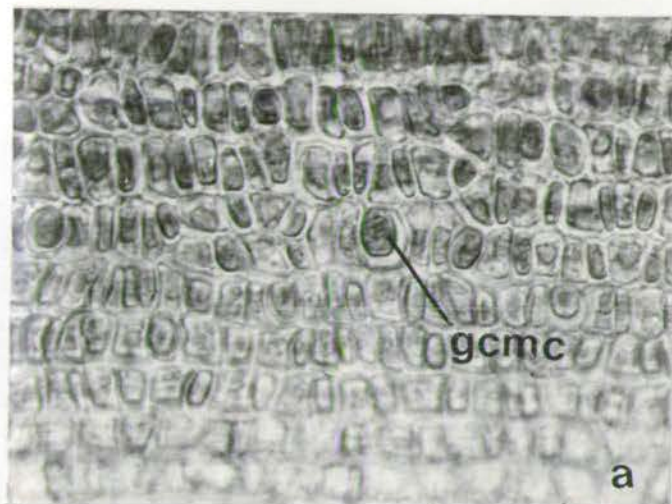


PLATE 9. STAGES IN THE STOMATAL DEVELOPMENT - II.

Explanation in the text.

a. - 1. Boesenbergia sp. (B & M 5164)

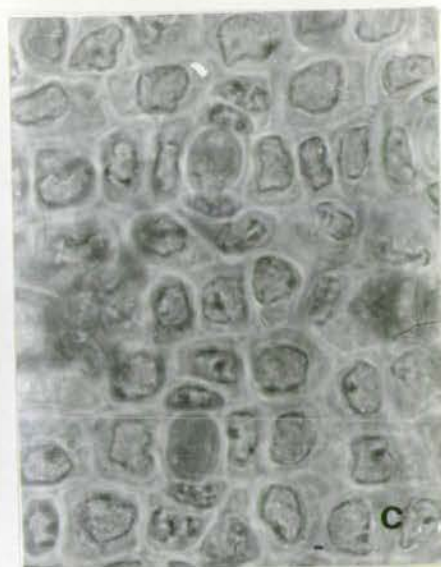
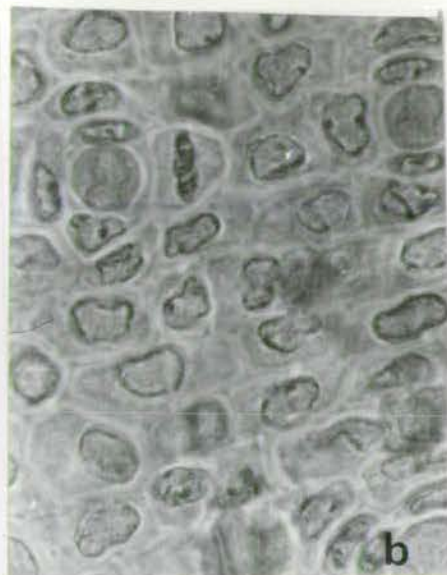
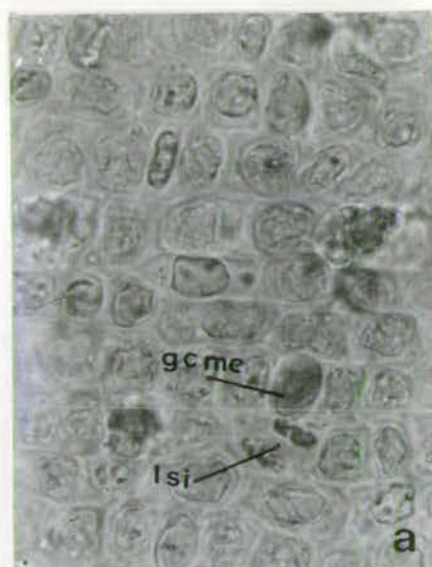
g.c.m.c. = guard cell mother cell.

l.s.i. = lateral subsidiary cell initial

l.s₁ = first produced lateral subsidiary
cell dividing.

Figures a-c x c.680; d-i x c.970

107
Plate 9



do divide more than once or the first formed subsidiary cell may divide again and the result is two or more polar subsidiary cells on either side of the guard cells. These last divisions of the polar subsidiary cells increases the number of the subsidiary cells around the stomata to between 6-8, or occasionally more than eight.

The development of the stomata is complete when the guard cell mother cells have divided. The other epidermal cells are enlarged, vacuolated, and the nuclei become gradually smaller in size. The oil cells differentiate without any division and the hairs elongated rapidly and remain unicellular. Although there were no living specimens for the study of the development of branched unicellular hairs of Renealmia, it is supposed that, since these hairs are unicellular and aseptate, their development would be similar to that described above. The branchings may be produced earlier in the differentiation when the apical papillae might have branched in different angles. However, the development of these branched hairs are worth investigating where the living materials are available.

DISCUSSION.

The development of the stomata and epidermal structures for thirty-six species, in sixteen genera of the Zingiberaceae, has been described. The mode of stomatal development is similar in all the parts of the plant investigated and this observation supports those of Stebbins and Khush (1961). This study disagrees with Tognini (1897) who reported that several modes of stomatal development may occur in different organs of the same plant. The development of the stomata is perigenous and the stomata are structurally and developmentally tetracytic and polycytic. Occasionally however, true paracytic

stomata may be found as in Cenolophon sp. (B 2268).

It is true, according to Paliwal (1969) that the arrangements of the cells in the mature stomata often conceal the developmental relationships between the subsidiary cells and their precursors. In the Zingiberaceae, the number of the subsidiary cells of the stomata in the tribe Alpinieae is much less obvious than it is in the other tribes, i.e. Globbeae, Hedychieae and Zingibereae (Zingiber). In all the tetracytic stomata, the lateral subsidiary cells are very distinct and unmistakable from the adjacent epidermal cells, but probably the area of confusion is the nature of the polar cells which flank the guard cells on either side. This probably lead to the two lateral subsidiary cells reported for the unidentified Amomum sp. and Zingiber sp. by Stebbins and Khush (1961). Actually, the polar subsidiary cells are distinct, at least, slightly, and easily recognisable as part of the stomatal complex in the tribes Globbeae, Hedychieae and Zingibereae (Zingiber). But in the tribe Alpinieae, it is usually very difficult, particularly from the mature epidermis, to recognise the polar cells and subsidiary cells. Whereas these cells are developmentally subsidiary cells (see Plates 8 and 9), their relationships with both their precursors and the guard cells appear to be overshadowed by the nature of the overall cellular activity of the epidermal cells. As described earlier on, because of the prolonged meristematic activities of the protodermal cells, cells produced, including the polar subsidiary initials, become narrower at each stage. The result of this activity is that by the time the polar subsidiary cells are produced, they become narrow and elongated transversely in a similar pattern to the adjacent epidermal cells. These polar subsidiary cells, apart from the fact that they flank the guard cells, may be difficult to distinguish from the

epidermal cells. Therefore the difference between the stomatal complex of the tribe Alpinieae, and those of the other tribes, is probably in the higher cellular activity which leads to higher frequency of epidermal cells and stomatal index in the Alpinieae than in the Hedychieae, Globbeae and Zingibereae. Also there seems to be a gradual increase in the stomatal specialisation, in terms of the number of subsidiary cells and their distinction from the adjacent cells, from the Hedychieae through the Globbeae and Zingibereae to the Alpinieae. The evidence for this is discussed later (page 171).

The observations made particularly in the tribe Alpinieae disagree with the theory of Bunning (1952, 1956) about the inhibitory zones around the developing stomata. In this theory, Bunning suggested that the developing meristemoid inhibits other cells within a certain range from turning into meristemoids. In the Alpinieae, as a result of the prolonged meristematic activities of the protodermal cells, many new meristemoids are produced by the protodermal cells in between the early formed meristemoids, and occasionally younger meristemoids may be produced close to or in contact with these older meristemoids (see Plate 9). Furthermore, these later formed meristemoids do develop into normal mature stomata and become interspersed among the older stomata. The frequent presence of contiguous stomata in the species examined is probably an evidence against the inhibitory theory. Various contiguous stomata, such as those with their guard cells in contact, or where two pairs of guard cells share the lateral or polar subsidiary cells between them, have been observed in some species. Therefore, if there is anything like the inhibitory influence, according to Pant and Kidwai (1967), these contiguous stomata would not have been formed, or it might be that the inhibitory influence was overcome or removed where such stomata were produced.

The polycytic stomata observed in Boesenbergia and some species in Kaempferia and Camptandra are very similar structurally and developmentally to those of the family Costaceae.

Stebbins and Khush (1961), after considering a number of characters and their relationship or correlation with the stomata types in the monocotyledons, came to the conclusion that stomata with many subsidiary cells, i.e. more than two, are primitive and those with two or none were derived by the reduction in the number of subsidiary cells from the stomata with many subsidiary cells. Within the Zingiberaceae, although the stomata is predominantly tetracytic, and hence primitive, there is a gradual specialisation from the most primitive (with 5-8 subsidiary cells) to the advanced type (with fewer than 4 subsidiary cells). If the above conclusion is tenable, the genus Boesenbergia, at least within the materials available, whose species have the highest frequency of polycytic stomata, is probably the most primitive in this respect.

In the Alpinieae, although stomata with 5-6 subsidiary cells are found occasionally, a higher trend in the specialisation of the stomatal complex takes place among its genera. The polar subsidiary cells gradually lose their structural identity as subsidiary cells in the mature stomata. And the evidence of the developmental relationships between these cells and their precursors can no longer be interpreted from mature cell alignment but could only be found in their developmental stages. Furthermore, the structural identity of these polar subsidiary cells is further overshadowed by the high cellular activity of the protodermal cells. This high cellular activity, according to Stebbins and Khush (1961), is an advanced characteristic. The highest level of stomatal specialisation within the family therefore, is probably found in some species such as Cenolophon sp. (B 2268). In this

species, paracytic stomata were observed and take about 25% of the total number of stomata present. The failure of the polar subsidiary cell initials either on both sides or on one, lead to the formation of paracytic stomata or those with one polar and two lateral subsidiary cells (i.e. tricytic stomata). The gradual loss of structural identity in the polar subsidiary cells of the Alpinieae and the presence of some paracytic stomata in Cenolophon sp. (B 2268) may be regarded as a transition between true tetracytic and exclusively paracytic condition. If any genus is to be described as the most advanced, as far as stomata are concerned, it should not be Zingiber and Amomum as suggested by Stebbins and Khush (1961), but those genera or species which possess the highest frequency of the specialised stages of the stomatal complex. In this case, the species of the tribe Alpinieae may be regarded as slightly more advanced than those in the other tribes. Although, there is no genus in the family whose stomata are exclusively paracytic, essentially the Cenolophon sp. (B 2268) possesses the factual transitional stages between the tetracytic and paracytic stomata.

INDUCTIVE MECHANISM.

In an attempt to explain the mode of stomatal development in the monocotyledons, Stebbins and Jain (1960) and Stebbins and Khush (1961) suggested that, an inductive stimulus, produced by the guard cell mother cell, attracts the nuclei of the adjacent cells (perigenes) and stimulates them to divide. Its influence is either on one side (unilateral), or both sides (bilateral), and may be manifested before or after the divisions of the nucleus of the g.c.m.c. The behaviour of the nuclei of the perigenes and g.c.m.c. observed in this study strongly support this inductive mechanism.

Throughout the family, it seems that the inductive stimulus is very active bilaterally in all the stomata and this leads to the production of the predominant tetracytic stomata. Furthermore, there may be local variation in the strength of the induction on the same epidermis or in the different species. The presence of some polycytic stomata in all the species examined probably supports this view. Furthermore, the inductive stimuli is probably more active laterally in most species of Boesenbergia than in any other genus.

The abnormal stomata are of interest in this context. It appears that, in some of the contiguous stomata observed in this investigation, such as the juxtaposed stomata with shared subsidiary cell (Plate 7.e), there is a counter-balanced effect of two opposite inductive forces on a single potential perigone. This probably leads to the disruption of the normal divisions so much that such perigenes either divide abnormally, producing more cells, orientated differently, or the cell wall between the new cellular materials may be dislodged or fail to form.

V. SPECIAL TAXONOMIC PROBLEMS AND THE ANATOMICAL CONTRIBUTIONS

Despite the fact that the delimitation of the genera within the family appears to be well defined on floral features, there are still some taxonomic problems arising as a result of the different systems adopted by different investigators. Some of these problems have been considered in the light of anatomical data obtained in this investigation. The problems examined here include:

- (A) Relationship between the African and Asiatic Kaempferia,
- (B) Taxonomic distinction and relationships of Renealmia,
- (C) Tribal position of Zingiber,
- (D) The anomalous species Hornstedtia leonurus.

The following discussions are the anatomical contributions to the understanding of these problems:

A. RELATIONSHIP BETWEEN THE AFRICAN AND ASIATIC KAEMPFERIAS.

The genus Kaempferia Linn. was established by Linnaeus in 1753. In 1862 the genus Cienkowskya was established by Solms Laubach (Sitzungsbericht der Ges. naturf. Freunde, July 1862) on a Zingiberaceous plant, Cienkowskya aethiopica, of Abyssinia (Ethiopia), which differs from Kaempferia in the following features: the inner perianth lobes are united so as to form one 3-lobed lip, which is split to the base posteriorly.

K. Schumann (1904) reduced this genus to sub-generic rank as one of the five sub-genera he recognised under Kaempferia. Some of these sub-genera have since been elevated to the generic rank, e.g. Sect. Monolophus. K. Schumann becomes Caulokaempferia Larsen (1964), and some of the species of sub. genus Soncorus Horan. have also been separated under the genus Stahlianthus.

Recently, in 1964, at the Xth International Botanic Congress, Edinburgh,

Drs. Spearing and Mahanty, who had studied the cytology of some of the African and Asiatic Kaempferias, suggested that the African species should be regarded as a distinct genus under the name Cienkowskya. They based their suggestion on the differences between these two groups of species in floral structures and the basic chromosome number. The Asiatic species show a preponderance of the basic number as $n = 11$, whereas the African species show a basic number of $n = 14$, except for one species, Kaempferia brachystemon, with diploid number $2n = 26$.

As has been seen in dealing with individual features, the African species are distinct anatomically from the Asiatic species in a number of ways. The leading difference between the two is the presence of stigmata in the former and their absence in the latter. Apart from this, there are other differences between them, these are listed below:-

Summary of the differences between
Cienkowskya and Kaempferia

<u>Characters</u>	<u>Cienkowskya</u>	<u>Kaempferia</u>
1. Lateral staminode.	Connate to labellum.	Free or partially free.
2. Ligule shape and size.	Entire; up to 6 mm.	Auriculate; up to 3 mm.
3. Sheath T.S. Arc II and III.	Few or absent.	Well developed.
4. Petiole T.S. Arc II and III.	Few or absent.	Well developed.
5. Hypodermis.	Absent or poorly represented.	Well developed 1-2 layers on both surfaces.
6. Veins.	Extend from abaxial to adaxial epidermis.	Attached to either adaxial or abaxial only or independent of both.
7. Internal stigmata in sheath and lamina.	Present.	Absent.

<u>Characters</u>	<u>Cienkowskya</u>	<u>Kaempferia</u>
8. Adaxial and/or abaxial epidermis.	Not papillate.	Papillate.
9. Cytology - basic chromosome No.	n = 14, (13 in few cases).	n = 11
10. Distribution.	African.	Asiatic.

As it is evident from the above differences, there is little doubt about the distinction between the African and Asiatic Kaempferias, and the separation of the former as a distinct genus, Cienkowskya, is fully supported on anatomical grounds. This old generic name should be re-established for the African species which has earlier been published under the name Kaempferia.

B. TAXONOMIC DISTINCTION AND RELATIONSHIPS OF THE GENUS RENEALMIA.

The genus Alpinia was established by Linnaeus (1754) who based his descriptions of this genus on the species Alpinia racemosa from tropical America. This was the only species he described. Later, the genus Renealmia was established by the younger Linnaeus (1789) and his type species, also from tropical America, was Renealmia exaltata. Subsequently, the Asiatic and American species were referred to both genera up to the monograph of Horaninow, 1861. The taxonomic distinction between the two genera was uncertain and there was no agreement among workers concerning this. Later investigators, including Schumann (1904), considered the type species of Alpinia and Renealmia to belong to one genus, but gradually, the name Alpinia came to be used mainly for the Asiatic species. Renealmia was adopted for the tropical American and West African species and Alpinia for an assemblage of species which did not include the type species A. racemosa.

The American botanists regularised this unsatisfactory taxonomic situation by proposing the conservation of the name Renealmia for the American and West African species. Alpinia Roxb. has been conserved, with A. galanga as type species for the Asiatic plants.

Recently, Holttum (1950), expressed some surprise as to the close similarities between the descriptions of the inflorescence axes of the section Dieramalpinia of Alpinia and the genus Renealmia as was described by Schumann (1904). The two are so similar in the descriptions that any casual worker might easily mistake one genus for the other. However, upon detailed examination of two species of Renealmia from South America, Holttum came to the conclusion that Renealmia should be maintained, although the differences are slight.

The fifteen species of Renealmia examined in this study show the presence of many anatomical features in common with Alpinia species, which belong not only to the section Dieramalpinia but to other sections as well. Such anatomical similarities include the presence of hypodermal fibres in the lamina which is almost characteristic of Renealmia but present in a number of species of Alpinia and some other genera, e.g. Amomum and Aframomum.

The only anatomical feature which seems to distinguish the two genera is the presence of branched/stellate hairs in Renealmia. This type of hair is absent from any of the species of Alpinia examined in this study and it has never been reported in the literature. The presence of these hairs in the species of Renealmia from all over its range of distribution, i.e. on species from America and West Africa, is evidence in support of the naturalness and distinctiveness of this genus.

Similar hairs have been described above in two species of Rhynchanthus and Riedelia sp. (Millar 14594). These genera are florally distinct and do not affect the problem of Alpinia and Renealmia.

C. TAXONOMIC POSITION OF ZINGIBER BOCHM.

The taxonomic position of the genus Zingiber appears to be the most uneasy in the history of the classification of the family. With the different systems proposed for the family, the genus has alternated between the tribes Hedychieae and Zingibereae. Engler and Prantl (1930), and K. Schumann (1904) following O.G. Petersen (1889), placed Zingiber in the tribe Zingibereae which includes most of the genera now recognised under the tribe Alpinieae (sensu Holttum 1950).

The recent change in the tribal position of Zingiber was that made by Holttum (1950). He proposed that the genus should be included in the Hedychieae in which, as he suggested, it has a natural place. The main characteristics of the tribe Hedychieae upon which this proposal was based lies in the development of free lateral and petaloid staminodes in the Hedychieae, whereas these are rudimentary in the Alpinieae (i.e. K. Schumann's Zingibereae without Zingiber). Although these staminodes occur in Zingiber, they are adnate to the labellum and never free. Because Holttum's new group Hedychieae (i.e. plus Zingiber) is different from Schumann's Zingibereae, Holttum retained Hedychieae as the tribal name, and renamed the remaining genera in the Zingibereae (minus Zingiber) under the tribal name Alpinieae.

Recently, Tomlinson (1956) has pointed to the naturalness of Zingiber within the Hedychieae because, like all other characters, it shares the median distichy of the leaves with the genera in the tribes Globbeae and Hedychieae.

Since Zingiber is the type genus for the family the inclusion of it in a tribe with a different tribal name other than that derived from its own name, is not in keeping with the Code of Botanical Nomenclature (Art. 19).

Zingiber is clearly closer, in many of its characteristics, to the

Hedychieae than Alpinieae. The following are the differences between Zingiber and the Hedychieae:

<u>ZINGIBER</u>	<u>HEDYCHIEAE</u>
1. Lateral staminodes adnate to labellum; style extended beyond anther lobes, upper part enfolded in elongate anther-crest; stigma protruding at tip.	Lateral staminodes free; style not extended beyond anther-lobes; stigmata protruding at top of these; anther-crest if present, short and flat.
2. Petiole swollen, pulvinus-like, vascular bundle with collenchymatous sheath.	Petiole not pulvinus-like, vascular bundles with sclerenchymatous sheath.

The features enumerated above are considered to be enough for the exclusion of Zingiber from either the Hedychieae of Holttum or the Zingibereae of other workers. While full investigation is essential for a sound revision of this genus, its separation into a tribe of its own under the name Zingibereae (*sensu stricto*) is recommended. This is considered as the most appropriate change that is necessary in view of the exceptional position this genus has been assigned in the past classifications. If this suggestion is acceptable, it means that the family is now composed of four tribes, viz:- Globbeae, Hedychieae, Zingibereae and Alpinieae. This new arrangement might eliminate the lengthy descriptions or definitions that might be necessary because of the newly available vegetative and anatomical characters.

D. THE ANOMALOUS SPECIES HORNSTEDTIA LEONURUS (Koenig) Retz.

The species Hornstedtia leonurus is a peculiar species among the others in the genus Hornstedtia. Holttum (1950) discussed in detail the floral peculiarities of this species and the following descriptions were taken from his work, "Each bract encloses two flowers, and these are arranged, with their bracts (bracteoles) exactly like the flowers of a cincinnus in Alpinia or Geostachys." These features, according to Holttum, show that H. leonurus has retained two primitive characters which have been lost by the other species in the genus.

During this study, observations show that this species is unique anatomically, not only within the genus Hornstedtia, but in the family as a whole. This is because the presence of the prickly-like sclereids in the leaf sheath, petiole, and to some extent, in the midrib of the lamina, have not been found anywhere else. This species is also peculiar within the genus Hornstedtia in that it is the only species in which the sclerotic phloem elements, which is almost a generic characteristic for the genus, is absent. It is very interesting to note that it is the only species in Hornstedtia which has some distinctive anatomical characteristics in common with the genera Achasma, Phaeomeria, and Elettaria. First, it resembles Elettaria and Achasma in the median ('inverted triangle') arrangement of the Arc III and IV vascular bundles in the adaxial side of the petiole, although sometimes a very clear distinction may not be easily obvious as in some species of Amomum and Geostachys. Secondly, it is similar to Achasma, Elettaria cardamomum, and a few species of Alpinia in the presence of small vascular bundles (Arc IV) or fibrous strands which are close to the adaxial surface of the midrib of the lamina.

On the basis of the differences in the floral characteristics, Holttum

has speculated that this species might be separated into a new genus. This suggestion is strongly supported by the anatomical peculiarities of this species.

VI. TAXONOMIC EVALUATION OF VEGETATIVE AND ANATOMICAL CHARACTERS.

The vegetative and anatomical characters that may be of some diagnostic and taxonomic value will be discussed according to their patterns of occurrence, full details of which are presented in Table 5.

(I) Characters that are more or less uniform throughout the family.

The family Zingiberaceae is characterised by the following features:-
Aerial stem unbranched; true stem developed, a non-fluted fibrous cylinder present within the stem. Leaves distichous; leaf sheaths long, open, but overwrapping on the opposite side to the lamina insertion, at least at the base. Ligule open. Single row of abaxial air canal systems present in the leaf axis. Oil cells present in all the species and silica bodies in most of the genera. Starch grains simple and flattened.

The characters mentioned above distinguish the family from Costaceae, and probably from all the other families in Zingiberales.

(II) The family is probably divisible into the following four tribes:-
Globoseae, Hedychieae, Zingiberaceae (new proposal see page 179) and Alpinieae.
The tribes in general lack absolutely diagnostic anatomical features, but nevertheless some support is given.

(a) The distinctiveness of the tribe Zingiberaceae (sensu stricto) has been discussed (see page 179).

(b) The tribe Alpinieae is almost characterised by the presence of stegmata in most of its species. Previously, it was thought that stegmata might be exclusive to this tribe, but internal stegmata are also present in the genus Cienkowskyia (African Kaempferias), and in Globba leucantha and G. pendula. The occurrence of the stegmata elsewhere as mentioned here reduces its diagnostic value for the tribe Alpinieae.

(c) Fleshy rhizome and/or tuberous roots are characteristic of the

genera of the tribes Globbeae, Zingibereae and Hedychieae except Scaphochlamys and Burbridgea; whereas, the genera of the tribe Alpinieae are characterised by less fleshy or woody rhizomes and fibrous and/or stilt roots.

(III) Characters that are common to some groups of genera and therefore helping to characterise them.

(a) The absence of fibrous cylinder in the true stem, although this may be developed in the inflorescence axis, is diagnostic for Globba, Mantisia and Caulokaempferia.

(b) The following genera: Scaphochlamys, Curcuma, Hitchenia, Kaempferia, Haplochorema, Cienkowskya, Boesenbergia, Stahlianthus and Camptandra are characterised by:- a more or less loose pseudostem; poorly developed fibrous cylinder which is often short or absent; + erect sheath which is frequently channelled; similar petiole and midrib anatomy. All except Curcuma and Hitchenia have delicate hairs whose bases are collapsible. The individual genera may be separated on some distinctive features. All the genera mentioned above are different from the rest of the tribe Hedychieae. The remaining genera, i.e. Hedychium, Brachychilum, Roscoea, Cautleya, and Burbridgea, apart from the general fundamental features, do not have such group characters in common except for Hedychium and Brachychilum.

(IV) Characters that are of limited or restricted occurrence in certain genera. This type of character is useful for the generic delimitation. The following are examples:

(a) The collenchymatous bundle sheath in the petiole of Zingiber is unique and has been discussed above.

(b) Branched/stellate hairs are of restricted occurrence and are characteristic of Renealmia and two species of Rhynchanthus and one Riedelia sp.

(c) The genus Hornstedtia is unique in the presence of sclerotic phloem parenchyma cells in the vascular bundles of the leaf axis, except in H. leonurus.

(d) The absence of the Arc II bundles in the abaxial position in the sheath and midrib of Roscoea, but with the vascular bundles of similar sizes pectinating with the Arc I bundles and air canals, is diagnostic for this genus. Few Arc II bundles, about 2 - 3, are present in the median part of the transverse sections of the sheath of Caulokaempferia and Camptandra. Cienkowskya is also characterised by the absence of Arc II bundles in the sheath.

(e) The single adaxial row of Arc IV bundles with the prominent development of abaxial Arc II in the petiole is diagnostic for Globba.

(f) Roscoea is characterised by the presence of 'bulliform' or papillate cells on the midrib of the lamina.

(g) The papillate adaxial and/or abaxial epidermis is diagnostic for Kaempferia (Asiatic species) and a few species of Boesenbergia. This is absent from the African Kaempferias (Cienkowskya),

(h) The species Hornstedtia leonurus is unique in the genus as well as in the family in the presence of prickly-like sclereids in its leaf axis.

(i) The presence of inflated bristles is probably diagnostic for the species Hitchenia careyana.

(V) Characters of sporadic occurrence (perhaps in one or two species of scattered genera) and therefore not of general value in classification, but of some diagnostic importance. The examples are:-

(a) Mechanical tissues were observed in the sheath, petiole and lamina of some species in the different genera of the tribe Alpinieae. The diagnostic

value of this character is reduced because it is absent from many of the species in the tribe and that it is present in some species of another different tribe.

However, the variations in the nature of the mechanical tissue may be useful for specific separation within a genus such as in Hornstedtia. In this genus there are differences among the species in the position and constituent tissues of the mechanical zone (see page 57).

(b) The walls of the costal cells are almost sinuous in some species of the following genera:- Elettaria, Achasma, Geocharis, Rhynchanthus, Amomum and Alpinia.

(c) Abaxial palisade-like cells are present in a number of the species of Scaphochlamys and Boesenbergia.

(VI) Characters that may be of value in one part of the family, but occur more or less sporadically elsewhere.

(a) Adaxial hypodermal fibres in the lamina are a constant character for all the fifteen species of Renealmia examined, but this feature is also present in a few species of Elettaria, Riedelia, Amomum, Aframomum, Alpinia and Cyphostigma.

(b) Furthermore, the presence of costal cells that are transversely elongated, i.e. with long axis perpendicular to the veins, is probably characteristic of the genus Renealmia, but it occurs also in few species of Globba, Zingiber, Amomum and Alpinia.

(c) The genus Achasma is probably characterised by adaxial vascular bundles belonging to Arc IV system in the lamina. This feature also occurs in Hornstedtia leomurus, some species of Alpinia and Amomum.

(d) Costal cells with circular secondary walls are present in most species of Cautleya, but similar cells have been observed in Rhynchanthus beesianus

and a few species of Alpinia.

GENERAL CONSIDERATIONS

The patterns of occurrence of the anatomical characters point to some salient facts about the usefulness of these characters in the classification of the family.

The evidence shows that the family is characterised anatomically. If the vegetative and anatomical characters are considered alone, the two families Zingiberaceae and Costaceae are distinct from each other as they are in their floral characteristics.

Within the family, the tribes are weakly characterised^{anatomically}. This is perhaps a reflection of their rather weak characterisation morphologically. For instance, the presence of stigmata in the Alpinieae is a weak character because it is absent in some of the species or genera in this tribe, and already known in one genus and two species belonging to the other tribes Hedychieae and Globbeae respectively.

Certain groups of genera have some anatomical features in common, especially where the group is defined by growth pattern such as in the short-stemmed genera in the Hedychieae. In the whole family, the number of genera that are well characterised by individual distinctive anatomical characteristics is quite small.

For the rest, there are characters that occur either uniquely or sporadically in the family. These are not useful for classification but may be of value in identification. Such characters may not be useful for numerical analysis because they may produce a muddling effect on a classification. Sporadic occurrence is in most cases presumably due to the independent origin of the

of the characters concerned. These are presumably the characters that are not concerned with the main evolutionary trends within the family.

LIST OF VEGETATIVE AND ANATOMICAL CHARACTERS.No.

1. Rhizome fleshy, swollen.
2. Rhizome not fleshy, but fibrous and/or woody.
3. Rhizome contracted.
4. Root tuberous.
5. Root fibrous, and/or woody.
6. Stilt roots present.
7. Plant tall, pseudostem more than 1 metre.
8. Plant short, pseudostem less than 1 metre.
9. True stem well developed, more than $\frac{1}{4}$ of the pseudostem.
10. True stem poorly developed or absent, usually less than $\frac{1}{4}$ of the pseudostem.
11. Sheath closely clasping.
12. Sheath more or less loosely clasping, erect and separate.
13. Sheath surface with raised transverse veinlets.
14. Sheath surface with bunches of velvety hairs.
15. Ligule entire.
16. Ligule bilobed, lobes round or obtuse.
17. Ligule bilobed, lobes triangular or acute, long, (more than 2 mm. long).
18. Ligule bilobed, lobes triangular or acute, short, (less than 2 mm. long).
19. Ligule auriculate, lobes short.
20. Ligule broad/emarginate.
21. Ligule as membranous narrow collar inside the base of petiole or lamina.
22. Petiole long, more than 25 mm. long.
23. Petiole short, less than 25 mm. long.
24. Petiole absent, i.e. lamina and sheath confluent.
25. Petiole channelled.
26. Petiole with small raised 'mounds' on its sides near the base.
27. Petiole 'pulvinus-like'.
28. Lamina adaxial surface variagated.
29. Indumentum on the adaxial surface of the lamina.
30. Root with thick fibrous tissue in the cortex.
31. Endodermis well thickened.
32. Fibrous cylinder developed in the stem to about more than $\frac{1}{2}$ the pseudostem height.

33. Fibrous cylinder absent from the stem, but may be developed in the inflorescence axis.
34. Arc II absent from the sheath.
35. Arc II if present, few, about 1 - 3 in the median part of sheath.
36. Mechanical tissue present in the sheath.
37. Petiole vascular bundle sheath collenchymatous.
38. Petiole with a single adaxial row of Arc IV.
39. Petiole with median triangular Arc IV arrangement.
40. Petiole with Arc II bundles or few (1 - 3).
41. Petiole with few Arc III and IV.
42. Petiole with abaxial mechanical tissue.
43. Petiole with adaxial mechanical tissue.
44. Lamina midrib cells papillate in surface view.
45. Lamina midrib with abaxial mechanical tissue.
46. Lamina midrib with adaxial median sclerotic or fibrous tissue.
47. Lamina midrib with adaxial fibrous tissue flanked on either side by smaller subsidiary bundles and strands.
48. Lamina midrib with few smaller Arc IV bundles.
49. Lamina midrib with expansion cells.
50. Lamina adaxial epidermis papillate.
51. Lamina abaxial epidermis papillate.
52. Phloem cells in the leaf axis sclerotic.
53. Main veins in the lamina attached to both epidermises.
54. Main veins in the lamina attached to adaxial epidermis only.
55. Main veins in the lamina attached to abaxial epidermis only.
56. Veins independent of both epidermises.
57. Narrow plate of fibrous sheath developed to the adaxial epidermis.
58. Epidermal cells narrow, i.e. 2-many times wider than high.
59. Epidermal cells broad, i.e. + isodiametric, in transverse section, never more than twice as high as wide.
60. Hypodermis developed on both surfaces.
61. Hypodermis present on adaxial surface only.
62. Hypodermis present on abaxial surface only.
63. Hypodermal fibres adaxial.

64. Hypodermal fibres abaxial.
65. Mesophyll wide, i.e. many-layered.
66. Mesophyll narrow, + centric, i.e. few-layered.
67. Abaxial palisade-like cells present.
68. Costal cells modified abaxially.
69. Costal cells not conspicuously modified, i.e. epidermis + uniform.
70. Costal cells with circular inner walls.
71. Costal cells rectangular/square/or mixed with both.
72. Costal cells strongly transversely elongated or mixed with some square cells.
73. Costal cells with straight walls.
74. Costal cells with almost sinuous walls.
75. Intercostal cells hexagonal/strongly transversely elongated.
76. Intercostal cells hexagonal less strongly transversely elongated, isodiametric or mixed.
77. Intercostal cells rectangular, longitudinally elongated.
78. Polycytic stomata very frequent, more than 25% of the stomata.
79. Polycytic stomata present, but less frequent, less than 25% of the total stomata.
80. Branched/stellate hairs present.
81. Delicate hairs with collapsible bases present.
82. Inflated bristles present.
83. Prickle-like sclereids present.
84. Root hairs branched.
85. Silica bodies in costal cells (epidermal stegmata).
86. Silica bodies in internal cells or fibres (internal stegmata).

VII. EVOLUTIONARY TRENDS IN THE ZINGIBERACEAE

Vegetatively the Zingiberales form an easily recognised group of monocotyledons; the differences between the more primitive and the more advanced members are in detail rather than 'fundamental' characters. The plant body of Zingiberaceae may be regarded, perhaps, as a reduction from an arborescent form as Phenakospermum (Strelitziaceae); the rhizome of Zingiberaceae representing the reduced prostrate trunk of a Phenakospermum from which leaf shoots are developed. A somewhat analogous situation may often be observed in the propagating houses of the Royal Botanic Garden, Edinburgh, a segment of the normal erect slender trunk-like stem of Dieffenbachia (Araceae) or Dracaena (Idiaceae) is laid horizontally (as though it were a rhizome) on damp sand and in time produces leafy shoots.

While vegetative evolution within the Zingiberales may have been relatively slow, floral evolution may have been comparatively rapid from the actinomorphic six-stamened condition of Musa to the zygomorphic and monandrous state which is a constant feature of Zingiberaceae.

Tomlinson, (1962) has discussed the evolutionary trends in the Zingiberales, and Stebbins and Khush (1961) made some suggestions as to the primitive and advanced stomatal structures. The following is a summary of some of the morphological and anatomical features which have been considered for the purpose of this discussion. The direction from left to right is taken, tentatively though, to represent specialisation from primitive to advanced characters respectively:

- | | |
|------------------------------|------------------------------|
| 1. Tall habit. | Dwarf habit. |
| 2. True stem well developed. | True stem short or + absent. |
| 3. Extended internode. | Congested internode. |
| 4. Compact pseudostem. | Loose pseudostem. |
| 5. Rhizome stoloniferous. | Rhizome contracted. |

6. Root fibrous, non-tuberous.	Root tuberous.
7. Fibrous cylinder developed.	Fibrous cylinder poorly developed or absent in the stem.
8. Petiole bundle sheath collenchymatous.	Petiole bundle sheath sclerenchymatous.
9. Multiseriate hypodermis.	Uniseriate hypodermis or absent.
10. Longitudinal veins buttressed to both surfaces.	Veins + attached to either surface or independent of both.
11. Stomata with many subsidiary cells (4-8 cells).	Stomata with few subsidiary cells (4 cells).
12. Vessels with oblique perforation plate.	Vessels with transverse perforation plate.
13. Vessels with scalariform end plate.	Vessels with simple end plate.
14. Stegmata present (predominant in the Zingiberales).	Stegmata absent.

Within the Zingiberaceae, the two major tribes, Hedychieae and Alpinieae are differentiated particularly by the behaviour of the lateral staminodes. In the Hedychieae, the lateral staminodes are developed attractively, whereas they are much reduced in the Alpinieae. The development of petaloid staminodes is the alternative to gradual disappearance and sterilisation of the anthers and as a means of increasing the attraction to pollinators. It is difficult to say that one or the other state of development is more primitive. The two groups mentioned above may be regarded as containing two basic floral features from which further specialisation within the family might have arisen.

There are two major growth trends in this family:

(a) The separation of the inflorescence from the leafy frond. The genera with terminal inflorescence axis usually produce small but numerous flowers whereas large and fewer flowers are characteristic of those genera with separate inflorescences. The separation of the inflorescence axis resulted in the avoidance of many mechanical problems in the plants and permitted larger fruits and flowers.

(b) Adaptation to seasonal climate. Plants with woody rhizomes are usually tall and perennial plants which are found in less seasonal climatic zones. The rhizomes are non-fleshy as new growth takes place continuously over the year. Whereas, plants with fleshy rhizomes and tuberous roots have become adapted to varying seasonal climates, hence the fleshy dwarf habit. Tuberous roots are particularly of an advantage because these storage organs can persist during the unfavourable season - dry in the tropical conditions in which Globba and Kaempferia are found, or cold in the temperate regions which Roscoea and Cautleya inhabit.

The reduction in the plant habit as an adaptation to seasonal changes probably affects the anatomy of the plant, particularly the development of the true stem and fibrous cylinder inside it. In the tall or stout plants, the internode is well extended and the fibrous cylinder is well developed. With the reduction in the stem size, the need for mechanical tissue becomes less important as other features probably of more significance for survival, become more important. This trend is probably obvious in the development of a short true stem and poor development or loss of the fibrous cylinder in the dwarf genera of the Hedychieae. These plants grow rapidly and reach their maturity within a short period of time, whereas, the tall Alpinieae plants develop strong mechanical tissue to support the plant which grows gradually and over a long period.

Furthermore, this trend is presumably correlated with the quick development and maturity of the stomatal and other epidermal structures in the dwarf genera, ^{compared} with the prolonged meristematic activity in the tall plants.

The nature and distribution of collenchymatous tissue in the plant probably suggest that it is a primitive feature. But its presence in the

bundle sheath of the petiole might be an adaptation to environmental conditions. This tissue may have arisen twice independently. Its presence in both Zingiber and Costaceae is not necessarily a sign of close affinity.

Tomlinson (1962) suggested that the multi-seriate hypodermis is probably more primitive than the uniseriate hypodermis or its absence in the plant; also that the attachment of the veins to both lamina epidermises precedes the independence of these veins from the surfaces. The presence of two or more hypodermal layers in the dwarf genera may be associated with the adaptation of the plants to certain environmental conditions rather than a primitive state. The gradual independence of the veins from either or both of the epidermises might be a derived condition, as it appears to be correlated with the small size in those plants found in the areas with seasonal changes.

The whole family, with the predominant tetracytic stomata, is relatively primitive amongst monocotyledons. But within the family the trends in the specialisation of the stomatal structures appear to be in the opposite direction to those of other features. Stomata with more than four subsidiary cells are more frequent in some of the dwarf genera, e.g. Boesenbergia, Camptandra, than elsewhere in the family.

Cheadle (1944 a,b; 1953, 1955), has discussed in great detail the trends in the specialisation of the tracheal elements in the monocotyledons. Accepting his principles, the Zingiberaceae are primitive in that vessels are confined, or more frequent in the roots than in any other part of the plant. This family shares this feature with many other families in the Zingiberales and such families as Bromeliaceae, Agavaceae, Araceae, to mention a few.

Within the family, the trend in the specialisation of the vessels seems to be correlated ^{with} the plant habit. More advanced stages of vessels are

found frequently in the tall plants of the Alpinieae than in the dwarf genera of the Hedychieae. The former plants probably need more efficient conducting system than the latter and hence the frequency of advanced vessels in them. It is not, therefore, surprising that the progression in the vessels is in the opposite direction to other features in the family.

The presence of the stigmata is a predominant feature in the Zingiberales, and its absence from any plant should be a derived condition. The exact function of these silica bodies is not known, but they are chemical substances produced as a result of the physiological processes in the plant. The frequent absence of stigmata in Hedychieae might possibly be related to shorter duration of the leafy shoots. The plants have probably concentrated on other more important processes than the silica bodies which might not enhance their survival chances in the environments. However, the distribution of stigmata might possibly suggest that these structures have arisen more than twice within the family.

VIII. THE GENERIC GROUPINGS
AND THEIR CHARACTERISATION.

GROUPS OF GENERA:

SUB-DIVISION I

- I. GLOBBA, MANTISIA, CAULOKAEMPFERIA.
 II. SCAPHOCHLAMYS, CURCUMA, KAEMPFERIA, HAPLOCHOREMA, BOESENBERGIA,
STAHLIANTHUS, CAMPTANDRA, CIENKOWSKYA.

Sub-group:

- II. A. CURCUMA and HITCHENIA.
 II. B. KAEMPFERIA, HAPLOCHOREMA, BOESENBERGIA, STAHLIANTHUS,
CAMPTANDRA, Woods specimens.
 II. C. CIENKOWSKYA.
 II. D. SCAPHOCHLAMYS.
 III. HEDYCHIUM, BRACHYCHILUM, CAUTLEYA, ROSCOEAE, BURBIDGEA.

Sub-group:

- III. A. HEDYCHIUM and BRACHYCHILUM.
 III. B. ROSCOEAE.
 III. C. CAUTLEYA.
 III. D. BURBIDGEA.
 IV. ZINGIBER.

SUB-DIVISION II

- V. ALL GENERA OF THE ALPINIEAE (Sensu Holttum 1950).
 VI. Genera of uncertain position:-
CYPHOSTIGMA, ELETTARIOPSIS and ALPINIA PUMILA.

Considering the patterns of the occurrence and distribution of the anatomical features, it appears that it might be frustrating to rely on these features for the purposes of classification of the family. On this account, there are no such consistently variable anatomical features which would distinguish the major sub-divisions, i.e. tribes, within the family.

The groups described below have been composed of genera which, within the scope of this investigation, possess some distinctive features in common. These groups are essentially artificial because they have been based on fewer characters, and the arrangement is not intended as an alternative to the current sub-divisions of the family. Such groupings, however, might throw more light on the problems of the taxonomy of the whole family, or part of it. Furthermore, the distinctive anatomical features of certain genera will, no doubt, enhance other evidences from floral and cytological investigations.

GROUP I.

This group is distinctive morphologically and anatomically, because the three genera are composed of plants with slender aerial shoots which are usually less than 100 cm. tall; roots tuberous, but rhizome greatly contracted; leaves usually small in size; petiole short or lamina sessile; true stem well developed, slender. The absence of the fibrous cylinder in the true stem from the base of the plant up to the upper half, and the presence of this cylinder in the inflorescence axis, is probably the most distinctive anatomical feature for the group.

The individual genera are also distinctive one from the other in the following features:-

Globba is characterised by the production of vegetative bulbils on the

inflorescence axis; Ligule broad or emerginate. In the petiole the adaxial surface Arc IV bundles close to the adaxial/and the presence of abaxial Arc II bundles is characteristic of this genus. Hairs are bristles with stout bases and moderately thickened walls.

Two species of Globba are unique in the genus. These are G. leucantha and G. pendula which have internal stigmata in their lamina.

Mantisia is very similar to Globba in many of its anatomical features such as the petiole anatomy. But it is, however, different in some details. Vegetative bulbils have not been observed or reported for this genus, as it has been done for Globba. In the two species of Mantisia examined, there is one large Arc I vascular bundle in the centre of the midrib and its bundle sheath extends from the abaxial to the adaxial epidermis.

Caulokaempferia is distinct from the two genera mentioned above in the following features:- The plants are more slender and of tiny habit, up to 50 cm. tall. Ligule bilobed with triangular or round lobes or rarely entire, up to 8 mm. long. Arc II and III systems are poorly represented in the sheath and petiole and in fact, these are absent in the transverse sections of the sheath (fig. 6.F). This genus shares this absence or poor development of the Arc II and III bundles in the sheath with some species of Camptandra and Cienkowskya, where a similar situation was observed.

GROUP II.

The genera in this group share the following characteristics in common:- The group is distinctive because its components have a short, loosely clasping pseudostem; poorly developed true stem which may be short or absent; inflorescence axis composed of fewer number of internodes (2 - 3); fibrous cylinders feebly developed or absent but may be developed in the inflorescence

axis. This group may be sub-grouped into two:-

1a. Hairs stout bristles with thick bases and walls - Sub-group a:-

Curcuma and Hitchenia.

1b. Hairs delicate, filamentous, wavy or coiled, with thin walls and

collapsible bases - Sub-group b:- Kaempferia, Haplochorema,

Boesenbergia, Camptandra, Cienkowskya.

Curcuma and Hitchenia are easily recognised among the other genera by the presence of stout bristles on the plants. The ligules are usually small and inconspicuous.

Hitchenia is similar to Curcuma in most of the anatomical details. But Hitchenia careyana is different from H. glauca and any species of Curcuma examined in the presence of inflated bristles on the sheath and also in the presence of sclereids and/or sclerised cells in the abaxial hypodermis of the sheath. The abaxial epidermis of the lamina is papillate, as in most species of Kaempferia.

Scaphochlamys is distinctive because of the presence of a fibrous, non-fleshy rhizome and fibrous or stilt roots which are also not tuberous. The cortex of the root is composed of thick cells or sclerenchymatous fibres which form a fibrous cylinder in this zone.

Cienkowskya is also easily separated from the others in the group by:- Ligule entire; presence of internal stigmata in the sheath and lamina; hypodermis is poorly represented or absent and the veins extend to both epidermises in this genus.

Camptandra is different from the other genera in the group in that the pseudostem is less loosely compacted, the true stem developed to some extent although usually weak. A fibrous cylinder is present in the true stem.

Arc II vascular bundles absent or almost so in the sheath. In this feature, Camptandra is probably similar to Caulokaempferia and Cienkowskya.

The following genera, viz: Kaempferia, Boesenbergia and Haplochorema (H. uniflorum), have many anatomical features in common. Vegetatively, most species of Kaempferia are distinct, but anatomically they are similar to either Haplochorema uniflorum on one hand and some species of Boesenbergia on the other. For instance, Haplochorema uniflorum can be placed in either Kaempferia or Boesenbergia by employing different sets of characters

Kaempferia may be distinguished by the following features:- Petiole usually short, up to 5 mm. ^{or} rarely up to 60 mm. as in K. rotunda and K. ovalifolia; Ligule membranous, short, developed as narrow collar inside petiole base, up to 6 mm; auriculate with short lobes, a number, not all, of species with orbicular and/or variegated leaves. Other characters, such as papillate adaxial and/or abaxial epidermis, which are almost characteristic of Kaempferia, are present in some of the species in Haplochorema and Boesenbergia. These may not be useful for separating the three genera.

Haplochorema (H. uniflorum) may be distinguished from Boesenbergia by the slight bilobed or emarginate ligule whose lobes reach up to 1 mm. in length. Polycytic stomata are very frequent.

Boesenbergia may be recognised by the bilobed ligule with triangular or round lobes whose length varies between 3 - 15 mm. Polycytic stomata are very frequent in this genus, as in Haplochorema and some species of Kaempferia and Camptandra. Epidermis is narrow, 2-3 times as wide as high.

Woods, New Guinea specimens are distinguishable from the other genera and species in that the abaxial intercostal cells are rectangular, and longitudinally elongated. This type of cell is rather distinctive among the species

of the family. These specimens have yet to be identified.

GROUP III.

This group includes those genera which are distinct from those in Group II because they have compact pseudostems and the fibrous cylinder is well developed. But they are different from the genera in Group V in that they are either short plants, i.e. less than 1.5 metres tall, or their rhizomes are fleshy and/or roots tuberous.

Apart from the fundamental family features, these genera do not have many distinctive characteristics in common.

Hedychium and Brachyochilum are both very similar in their anatomical features. Their rhizome is fleshy, but tuberous roots are lacking or uncommon. Ligule large and entire. Transverse sections of sheath and petiole show that there are numerous, small vascular bundles representing all the Arcs I - IV.

Burbridgea is different from all others in this group in that the rhizome is not fleshy and the roots are fibrous, non-tuberous; the ligule is bilobed, lobes round and up to 25 mm. long.

Roscoea and Cautleya are easily distinguishable from the above genera by their tuberous roots. Roscoea is distinctive in the group and in the family in the following features:- Petiole absent, i.e. lamina and sheath confluent, the base of the lamina is indicated by a narrow and membrous ligule which is usually less than 3 mm; In the sheath and midrib, Arc II vascular bundles are absent from the abaxial position, but bundles of similar sizes pectinate with the Arc I bundles and air canals. The midrib cells are raised or papillate, a characteristic which is distinctive in the family, although

developed to a lesser extent in some species of Kaempferia.

Cautleya could be distinguished very easily from Roscoea because a petiole is present; ligule well developed, bilobed, lobes up to 7 mm. and may be unequal; some species have costal cells, some of which are with circular inner walls.

The lack of common distinctive characters among the genera in Group III probably suggests that the genera could be more usefully discussed by sub-dividing the group into natural sub-groups.

GROUP IV.

Only Zingiber belongs here.

This genus is distinctive in the morphology and anatomy of the petiole. The petiole is 'pulvinus-like', and the vascular bundle sheath is composed of collenchymatous tissue. In these characteristics the genus does not seem similar to any other in the family.

GROUP V.

This group is composed of all the genera of the tribe Alpinieae except Cyphostigma and probably Elettariopsis and Alpinia pumila.

The genera share a lot of morphological and anatomical features in common, so much so, that the reticulate pattern of the distribution of the characteristics makes it difficult to separate the individual genera. However, some genera are distinguishable because of the distinctive characteristics present in them, but the number of such separable genera is very small indeed.

Renealmia is characterised by branched/stellate hairs. Similarly, these hairs are present in Rhynchanthus beesianus, R. longiflorus and

Riedelia sp. (Millar 14594).

Hornstedtia is nearly unique in that the phloem parenchyma cells are sclerotic. This is not present in H. leonurus which is also unique in the presence of prickle-like sclereids in its leaf axis.

GROUP VI.

Genera of Uncertain Position.

Although I have examined one species of Cyphostigma, i.e. C. pedicellatum, the evidence from this study and from the literature shows that the loose pseudostem organisation found in this genus is similar to that of the genera in Group II. Also, Elettariopsis and Alpinia pumila have a similar pseudostem structure.

Cyphostigma pedicellatum shares the presence of hypodermal fibres in the lamina with most species in the Alpinieae including Elettariopsis curtissii (Tomlinson 1956, 1969). Moreover, the presence of abaxial sclerotic mechanical tissue in its sheath recalls those in Hitchenia careyana and most species of the Alpinieae.

ARTIFICIAL KEY TO THE MAJOR SUB-DIVISIONS
AND GENERIC GROUPS IN THE ZINGIBERACEAE
BASED ON VEGETATIVE CHARACTERS

- 1a. Plants of relatively short habit, i.e. usually less than 1.5 metres tall; rhizomes fleshy and/or roots tuberous (except Scaphochlamys, Burbridgea and to a less extent Boesenbergia); stigmata and mechanical tissue usually absent

SUB-DIVISION I

- 1b. Plants of relatively tall habit, i.e. frequently more than 2 metres tall (except Cyphostigma, Elettariopsis and Alpinia pumila); rhizomes usually non-fleshy, may be woody; roots fibrous or woody, stilt roots occasionally developed; stigmata and/or mechanical tissue may be present in a number of species

SUB-DIVISION II

SUB - DIVISION I

- 1a. Leaf sheaths closely clasping, forming a compact pseudostem; true stem well developed inside pseudostem
- 2a. Fibrous cylinder absent in the true stem; but may be developed in the inflorescence axis

GROUP I

(Globba, Mantisia and Caulokaempferia)

- 2b. Fibrous cylinder present in the true stem from the base to the inflorescence axis

- 3a. Rhizome fleshy and/or root tuberous

- 4a. Petiole 'pulvinus-like'; petiole bundle sheath collenchymatous

GROUP IV

(Zingiber)

4b. Petiole not 'pulvinus-like', bundle sheath sclerenchymatous

GROUP III

5a. Rhizome + massive and/or spreading; tuberous roots not common; numerous, small vascular bundles belonging to Arcs I-IV present in the sheath and petiole

SUB-GROUP IIIA

(Hedyehium and Brachychilum)

5b. Rhizome + contracted; roots tuberous; vascular bundles of Arcs I-III in the sheath and petiole relatively few and large

6a. Sheath and lamina confluent, petiole 0; ligule membranous and inconspicuous, less than 3 mm. long; Arc II bundles absent from the abaxial position in the sheath and midrib; midrib cells strongly papillate

SUB-GROUP IIIB (Roscoea)

6b. Sheath and lamina separated by short petiole; ligule + membranous at the upper half, up to 5 mm. long; Arc II bundles present in the abaxial position in the sheath and the petiole and midrib; midrib cells not papillate

SUB-GROUP IIIC

(Cautleya)

3b. Rhizome neither fleshy nor roots tuberous SUB-GROUP IIID (Durbridgea)

1b. Leaf sheath loosely compacted; true stem poorly developed, short or sometimes absent (except when the inflorescence axis is developed or may be present to some extent in some species of Camptandra)

GROUP II

7a. Rhizome fleshy and/or roots tuberous, stilt roots absent

8a. Hairs stout with thick bases and walls

SUB-GROUP IIA

(Curcuma and Hitchenia)

8b. Hairs delicate, with thin walls and collapsible bases

9a. Hypodermis usually well developed, at least represented by one

adaxial layer; veins usually attached to either epidermis or independent of both epidermises; stigmata absent from the plant; distribution in Asia, India, China, Philippines, New Guinea

SUB-GROUP IIB

(includes Kaempferia, Haplochorema,
Boesenbergia, Camptandra and
Stahlianthus)

- 9b. Hypodermis poorly developed or absent from the lamina; veins extending to both epidermises; stigmata present in specialised cells or fibres in the sheath and lamina; distribution Africa

SUB-GROUP IIC

(Cienkowskya)

- 7b. Rhizome fibrous, non-fleshy; stilt roots present, not tuberous

SUB-GROUP IID

(Scaphochlamys)

SUB-DIVISION II

- 1a. Branched/stellate hairs present

RENEALMIA

(+ Rhynchanthus beesianus,
R. longiflorus and Riedelia sp.
(Millar 14594))

- 1b. Branched/stellate hairs absent.

- 2a. Phloem parenchyma cells sclerotic

HORNSTEDTIA

(+ few species in Alpinia and Anomum)

- 2b. Phloem parenchyma cells not sclerotic

The rest genera of the tribe

Alpinieae

These genera are difficult to separate on the basis of vegetative and anatomical features alone

GENERA AND SPECIES OF UNCERTAIN POSITION

Plant with loosely compacted pseudostem, true stem not extended, short

Cyphostigma, Eletteriopsis and Alpinia pumila

ARTIFICIAL KEY
TO SOME OF THE GENERA IN THE ZINGIBERACEAE
BASED ON VEGETATIVE CHARACTERS

- 1a. Plants of relatively short habit, i.e. usually less than 1.5 metres tall;
rhizomes fleshy and/or root tuberous (except in Scaphochlamys and
Burbridgea)
- 2a. Leaf sheaths closely clasping, forming a compact pseudostem; true
stem well developed inside the pseudostem
- 3a. Fibrous cylinder absent in the true stem, but may be present in the
inflorescence axis
- 4a. Arc II and IV well developed in the sheath and petiole respectively;
Arc IV vascular bundles form an adaxial row close to the adaxial
surface of petiole 1. GLOBBA & MANTISIA
- 4b. Arc II represented by few (2-3) small vascular bundles in the
median portion of the sheath; Arc IV bundles are absent from the
petiole 2. CAULOKEAMPPERIA
- 3b. Fibrous cylinder present in the true stem from the base to the
inflorescence axis
- 5a. Rhizome fleshy and/or root tuberous
- 6a. Petiole 'pulvinus-like'; petiole vascular bundle collenchymatous
3. ZINGIBER
- 6b. Petiole not 'pulvinus-like'; petiole bundle sheath
sclerenchymatous
- 7a. Rhizome + massive, spreading, + partially subterranean;
tuberous roots uncommon; ligule entire; numerous, small
vascular bundles of Arcs I-IV in the sheath and petiole
4. HEDYCHIUM and BRACHYCHIUM

- 7b. Rhizome contracted, subterranean; root tubercous; ligule bilobed or developed as narrow collar inside lamina base; vascular bundles of Arc I-III in the sheath and petiole relatively few and large
- 8a. Sheath and lamina confluent; petiole 0; ligule membranous, inconspicuous, less than 3 mm.; Arc II bundles absent from abaxial position in the sheath and midrib; midrib cells strongly papillate, 'umbo-like'; costal cells with straight walls 5. ROSCOEIA
- 8b. Sheath and lamina separated by short petiole; ligule \pm membranous at the distal part, up to 5 mm. long; Arc II bundles present in the abaxial position in the sheath, petiole and midrib; midrib cells not papillate. Costal cells with circular outline in some species 6. CAUTLEYA
- 5b. Rhizome neither fleshy nor too tubercous 7. BURBIDGEA
- 2b. Leaf sheath loosely clasping; \pm separate and erect; true stem poorly developed, short or absent, sometimes when developed it may be slender and weak
- 9a. True stem slender and weak, up to 15 cm. long; fibrous cylinder present 8. CAMPTANDRA
- 9b. True stem short, less than 2.5 cm. from the base; fibrous cylinder usually absent from the short stem, except when the inflorescence axis is produced
- 10a. Abaxial hypodermis and/or epidermis of sheath sclerified and the sclereids may form a mechanical tissue in the sheath
- 11a. Hairs with greatly inflated bases present on the sheath; hypodermal fibres absent from the lamina 9. HITCHENIA (H. careyana)

- 11b. Hairs on sheath are bristles without inflated bases; adaxial hypodermal fibres present in the lamina

10. CYPHOSTIGMA (C. pedicellatum)

- 10b. Abaxial hypodermis and/or epidermis of sheath not sclerified; abaxial mechanical tissue absent

- 12a. Rhizome fibrous, non-fleshy; stilt roots often developed, cortex of root in t.s. with thick-walled fibres or fibre-like cells, roots not tuberous (except in Scaphochlamys Kunstleri)

11. SCAPHOCHLAMYS

- 12b. Rhizome fleshy and/or root tuberous; stilt root absent, root cortex with thin-walled cells, thick-walled fibres absent

- 13a. Stegmata present in specialised cells and fibres in the sheath and lamina; hypodermis poorly developed or absent from the lamina; veins extending to both epidermises; distribution in Africa

12. CLENKOWSKYA

- 13b. Stegmata absent from plant; hypodermis usually well developed, at least represented by one adaxial layer; veins usually attached to either abaxial or adaxial epidermis or independent of both; distribution in Asia, India, China, Philippines, New Guinea

- 14a. Hair stout with thick bases and walls

13. CURCUMA

- 14b. Hairs delicate, slightly wavy or coiled with thin walls and collapsible bases

- 15a. Abaxial intercostal cells rectangular, or \pm square in surface view; longitudinally elongated; sheath, petiole, and/or midrib may be 'keeled'; (distribution

in New Guinea)

14. Woods specimens (Woods 1732,
1549, 1151, 1562 & Cult. M. Black 1337;
and Alpinia sp ? Woods 1792)

15b. Abaxial intercostal cells hexagonal, ± isodiametric or
irregular; leaf axis not usually 'keeled';
distribution outside New Guinea or few spp. might be
found in this territory

16a. Ligule bilobed, lobes frequently triangular or round,
lobes up to 15 mm. long, some with tufts of small
hairs on the apex; polycytic stomata very frequent;
epidermal cells narrow as seen in transverse section,
(i.e. cell width 2-3 times their heights);
(adaxial and abaxial epidermal cells may be
papillate in some species)

15. BOESENBERGIA

16b. Ligule auriculate or entire, or as narrow membranous
collar inside the base of the petiole, lobes
triangular or round, short, up to 7.5 mm. long,
margins may be fringed by short hairs; polycytic
stomata may be frequent in some species; epidermal
cells relatively wide; width and height ± equal or
either slightly longer; adaxial and/or abaxial
epidermis papillate

16. KAEMPFERIA

(+ Haplochorema uniflorum)

1b. Plants of relatively tall habit, usually more than 2 metres tall;
rhizomes usually non-fleshy, may be woody; roots fibrous or woody, stilt
roots occasionally developed; stigmata and/or mechanical tissue may be

present

13a. Branched/stellate hairs present

14a. Adaxial hypodermal fibres present in the lamina

15a. Branched/stellate hairs with less than 10 branches; costal cells usually transversely elongated

17. RENEALMIA

15b. Stellate hairs with many branches, more than 10 in most cases; costal cells rectangular and longitudinally elongated

18. RIEDELIA SP. (Millar 14594)

14b. Hypodermal fibres absent 19. RHYNOCHANTHUS (R. beesianus, R. longiflorus)

13b. Branched/stellate hairs absent

16a. Phloem paranchyma cells sclerotic

20. HORNSTEDTIA

(except H. leonurus)

16b. Phloem parenchyma cells not usually sclerotic

17a. 'Prickle-like' sclereids present in sheath and petiole

21. H. leonurus

17b. 'Prickle-like' sclereids absent from sheath and petiole

18a. Ligule bilobed, lobes round

22. ADELMERIA

18b. Ligule usually entire, and if bilobed, lobes triangular

19a. Distribution in Africa

23. AFRAMOMUM

19b. Distribution outside Africa

24. Other genera in the ALPINIEAE

i.e. Alpinia, Amomum, Phaeomeria,

Achasma, Elettaria, Riedelia,

Plagiostachys, Geostachys,

Geocharis

S U M M A R Y

Vegetative material for about three hundred and five species belonging to about thirty-three genera in the Zingiberaceae were examined.

The occurrence, variation and different patterns of distributions of about eighty-six vegetative and anatomical characters are described and tabulated.

The contribution of the anatomical features to the taxonomy of the family is discussed. The family is characterised anatomically, but the separation of the tribes on the basis of anatomical features is weak. However, certain genera and species are characterised by their distinctive anatomical features. The following particular suggestions are presented:

- (i) That the African species of Kaempferia should be separated from the Asiatic species as the genus Cienkowskya. This suggestion is justified on both anatomical and cytological grounds.
- (ii) That the genus Zingiber be separated as a distinct tribe Zingibereae (sensu stricto). This genus has been taking an exceptional position in the past classifications. Its separation into a tribe of its own is supported by its unique anatomical characteristics.

Other contributions include the demonstrations of the anatomical distinction between the closely related genera Renealmia and Alpinia.

The stomatal development was studied in thirty-six species; it is always perigenous and the stomata are predominantly tetracytic. Polycytic stomata also occur but with less frequency, except in Boesenbergia and Camptandra where polycytic stomata are more frequent than the tetracytic type.

Certain evolutionary progressions within the family are suggested.

The genera are grouped together according to their anatomical similarities. Both an indented and a synoptic key is made for some of the genera.

A P P E N D I X A.

The following synopsis summarises the distribution
of some vegetative and anatomical characters in the family.

I. RHIZOME AND ROOT MORPHOLOGY

1. Rhizome often fleshy, and/or root tuberous:- Most genera in the tribes Globbeae, Hedychieae and the genus Zingiber (Zingibereae).
2. Rhizome not usually fleshy, may be woody; roots fibrous, never tuberous, may be woody, stilt roots occasionally developed:- Most genera in the tribe Alpinieae; and Burbridgea and Scaphochlamys.

II. VEGETATIVE AXIS

A. TRUE STEM:

1. True stem well developed, i.e. internode elongated to a variable height within the concentric pseudostem:- Most genera of the tribe Globbeae, Zingibereae, Alpinieae, and some mentioned in 2. below.
2. True stem poorly developed, i.e. internode not being well elongated, but + short and congested near the base of the plant:- Scaphochlamys, Curcuma, Hitchenia, Kaempferia, Haplochorema, Cienkowskya, Boesenbergia, Stahlianthus, Cyphostigma, Elettariopsis, Alpinia putnala; elongate to some extent in Camptandra.

B. PSEUDOSTEM:

1. Pseudostem very compact, leaf sheaths usually closely clasping and overwrapping:- Most genera except those under 2. below.
2. Pseudostem rather loose, leaf sheaths loosely clasping, + separate and erect from or near the base, sheath margins not often over-wrapping throughout their length:- Scaphochlamys, Curcuma, Hitchenia, Kaempferia, Haplochorema, Boesenbergia, Stahlianthus, Cienkowskya, Camptandra,

Cyphostigma, Elettariopsis and Alpinia pumila.

III. LEAF MORPHOLOGY

A. LEAF DIFFERENTIATION:

1. Lamina and sheath confluent:- Roscoea, Kaempferia gilbertii, K. angustifolia and Mantisia wardii.
2. Leaf usually differentiated into sheath, petiole and lamina:- Most genera in the family.

B. LEAF VARIEGATION:

Leaf lamina variegated:- Some species in Kaempferia, Zingiber zerumbet Alpinia sandarac. The variegation on the leaves of the last two species and Kaempferia gilbertii appears to be due to some chimera, probably of the sectorial type.

C. PETIOLE MORPHOLOGY AND SIZE:

1. Petiole usually very long and/or channelled:- Curcuma, Hitchenia, Scaphochlamys, Cienkowskya, Boesenbergia, Elettariopsis, Alpinia pumila and Cyphostigma.
2. Petiole usually short and less channelled:- Most of the other genera not mentioned in (1) above.
3. Petiole 'pulvinus-like':- Zingiber.

IV. ROOT ANATOMY

1. Root outer cortex usually sclerotic and lignified or thick fibrous tissue present:- Scaphochlamys, and most genera of the tribe Alpinieae.
2. Root endodermis with well thickened inner tangential and radial walls:- Most genera of the tribe Alpinieae and Scaphochlamys.
3. Endodermis usually less thickened, some with radial casparian thickenings

only:- Most genera of the Globbeae, Hedychieae and Zingiberieae.

4. Root hairs with some branched:- Hedychium gardnerianum, Hedychium x Raffillii and Kaempferia rotunda.

V. STEM ANATOMY

A. FIBROUS CYLINDER:

1. Fibrous cylinder developed in the stem, from the base to the inflorescence axis:- Most genera except those under (2) below.
2. Fibrous cylinder not usually developed in the stem, but may be present in the inflorescence axis:- Globba, Mantisia, Caulokaempferia, Kaempferia, Curcuma, Scaphochlamys, Cienkowskya, Boesenbergia and Haplochorema.

VI. SHEATH ANATOMY

1. Vascular Arc II absent from the abaxial position in the sheath, smaller bundles of similar sizes pectinate with the main Arc I bundles and air canals:- Roscoea, Kaempferia angustifolia.
2. Arc II system represented by a few (2 - 3) bundles in the median part of the sheath or absent:- Caulokaempferia and + Camptandra.
3. Vascular Arc II bundles present in the abaxial position in the sheath:- All the genera except those under (1) and (2) above.
4. Abaxial mechanical tissue in the sheath:- A number of species in the genera of the tribe Alpinieae and in Hitchenia careyana and Cyphostigma pedicellatum.
5. Abaxial hypodermis and/or epidermis of the sheath, petiole and/or midrib sclerotic:- Cyphostigma pedicellatum, Hitchenia careyana and most spp. in the tribe Alpinieae.

VII. PETIOLE ANATOMY

1. Petiole bundle sheath collenchymatous:- Zingiber.
2. Petiole bundle sheath sclerenchymatous:- All the genera except Zingiber.
3. Petiole with abaxial and/or adaxial mechanical tissue, sclereids or fibrous tissue:- Some species in most of the genera of the Alpinieae.

VIII. LAMINA ANATOMY

A. MESOPHYLL DIFFERENTIATION:

1. Lamina dorsiventral:- All the genera except perhaps some spp. in Scaphochlamys and Boesenbergia.
2. Lamina + pseudo-isolateral, i.e. with abaxial palisade-like layer along with the adaxial palisade and spongy layers:- Some species of Scaphochlamys and Boesenbergia.

B. MIDRIB ANATOMY:

1. Adaxial sclerenchymatous tissue present:- Achasia, some spp. of Alpinia, Amomum, Elettaria and Hornstedtia leonurus.
2. Phloem elements in leaf axis, particularly in the midrib and petiole, sclerotic:- Hornstedtia (except H. leonurus), one Amomum sp. (B. 5159 aff Xanthophebum), and Zingiber sp. (B. 4885 - epiphytic sp.).

C. EPIDERMIS IN T.S:

1. Adaxial and/or abaxial epidermis papillate:- Kaempferia, Haplochorema, few species of Boesenbergia.
2. Epidermal cells minutely papillate:- Kaempferia gilbertii, K. angustifolia and Hedychium gardnerianum.
3. Abaxial epidermis raised into shallow mounds or 'turrets' on which the stomata are situated:- Boesenbergia sp. (B. 4927).

Relative frequency of polytypic stomata less than 25%:- All other genera

D. EPIDERMIS IN SURFACE VIEW:

1. Costal cells often differentiated:- Most genera in the family except those under (2) below.
2. Costal cells not often very obviously differentiated:- Scaphochlamys except to a less extent in S. Kunstleri), some spp. of Boesenbergia, Woods specimens (aff. Boesenbergia).
3. Midrib cells elliptic, raised or papillate:- Roscoea; less well developed in Kaempferia and Boesenbergia.
4. Costal cells with circular inner walls:- Most species of Cautleya examined, but absent in some.
5. Costal cells almost sinuous:- Most spp. of Elettaria, Rhynchanthus, Achasma, Geocharis, Amomum, Alpinia.
6. Costal cells predominantly transversely elongated:- Renealmia, few spp. in Alpinia, Amomum, Zingiber, Elettaria.
7. Abaxial intercostal cells rectangular, longitudinally elongated:- Woods specimens, aff. Boesenbergia (plants from New Guinea).
8. Abaxial intercostal cells hexagonal, isodiametric, or slightly elongated transversely:- Most genera in the Globbeae, Hedychieae and Zingibereae.
9. Abaxial intercostal cells hexagonal, very strongly elongated transversely:- Most genera of the Alpinieae.

E. STOMATA:

1. Stomata tetracytic, although paracytic, tricytic and polycytic stomata may be present:- All the genera.
2. Relative frequency of polycytic stomata up to 40 - 75%:- Boesenbergia; few species of Kaempferia, Haplochorema, Camptandra and + Rhynchanthus.
3. Relative frequency of polycytic stomata less than 25%:- All other genera

except those under (2) above.

4. Relative frequency of paracytic and tricytic stomata up to 25 - 50%:-
Cenolophon sp. (B. 2268).

F. HYPODERMAL FIBRES:

1. Adaxial hypodermal fibres present:- Renealmia, few spp. of Alpinia, Riedelia, Amomum, Aframomum, Cyphostigma, Elettaria.
2. Abaxial hypodermal fibres present:- Alpinia allughas, Cenolophon oxymitrum (= Alpinia oxymitra).

IX. HAIRS

A. HAIRS UNICELLULAR, UNERANCHED:

1. Prickles:- Aframomum, Cenolophon sp.
2. Prickle-like sclereids or sclereid-like prickles:- Hornstedtia leomurus.
3. Bristles with rigid bases and shaft. All the genera except those under (4) below.
4. Delicate hairs, + filamentous, wavy or coily with thin walls and collapsible bases:- Scaphochlamys, Kaempferia, Camptandra, Boesenbergia, Haplochorema, Cienkowskya, and Zingiber.
5. Bristles with greatly inflated shaft near the basal half - ('balloon-like'):- Hitchenia careyana.

B. UNICELLULAR BRANCHED/STELLATE HAIRS:

1. Hairs with not more than 10 branches:- Renealmia, Rhynchanthus (R. beesianus, and R. longiflorus).
2. Hairs with many more than 10 branches, truly stellate, although branched hairs with 2 - many branches present (stellate hairs more predominant):- Riedelia sp. (Millar 14594).

X. CELL INCLUSIONS

SILICA BODIES:

1. Silica bodies in epidermal costal cells (epidermal stigmata) and/or in other epidermal cells present:- Most species in the tribe Alpinieae.
2. Silica bodies in specialised cells and fibres below the epidermis in the sheath and/or lamina (internal stigmata) (a) In both sheath and lamina:- Cienkowskiya (African Kaempferias), Alpinia javanica, (b) in the lamina only:- Globba leucantha and G. pendula.

APPENDIX B. VEGETATIVE REPRODUCTION

The production of vegetative bulbils was first reported for Globba by Schumann (1904). The presence of bulbils in most species of this genus is confirmed in this study. Vegetative bulbils were also observed for three other species, these are Hedychium greenii (fig. 34.B,C; Plate 10.a), Zingiber puberulum (fig. 34.D; Plate 10.c), and Z. incomptum.

It was observed that the nature of the formation of these bulbils is similar in the three species and Globba, except for few differences. It is common in the family that the first few floral bracts at the base of the inflorescence axes do not bear flowers (Holtum 1950). These floral bracts, however, protect dormant axillary buds (fig. 34.C). They remain dormant in most cases throughout the life of the inflorescence axis.

In Hedychium greenii, for example, such axillary buds increase in size as the inflorescence axis matures and the flowers begin to wither. At this stage, the buds become active (fig. 34.C) and their greenish colour becomes deeper. The buds increase rapidly in size and resemble a young developing rhizome element (fig. 34.B). The base is thickened or fleshy, and young adventitious roots are produced (fig. 34.B; Plate 10.a). The apical part continues to produce, at first, bladeless sheaths, and later, sheaths with expanded lamina are produced. There is a rapid change in the scale leaves which surround the swollen base of the bulbil. Some of these leaves turned brown and shrivelled in the same manner as on the developing rhizome element produced at the base of the plant.

The remains of the inflorescence axis are pressed to the centre (fig. 34.B; Plate 10.a), where two bulbils develop close to each other. The weight of these bulbils weigh down the frond until it touches or is near the ground level.

The bulbils are viviparous and are easily detachable by slight pressure on to the frond and they fall to the ground. If such bulbils land on a moist soil, the roots rapidly penetrate the soil and the shoot curves upwards to assume the erect position.

There is some slight difference between the bulbils in Hedychium greenii and Zingiber puberulum and Z. incomptum. In the two latter species, the mature vegetative shoot produces flowers on separate inflorescence axis at the base and not terminally on the plants. But, the frond at, or near, maturity gradually tapers to the apex, the leaves are gradually reduced in size from the middle and progressively to the apex where bladeless sheaths are produced (fig. 34.D). Such bladeless sheaths resemble either similar sheaths on separate inflorescence axis or the floral bracts of terminal inflorescence as in Hedychium and other genera. Meanwhile, the axillary buds become active and bulge out through the sheath or the latter may be pushed downwards by the growing bud. The buds rapidly develop in the same ways as described above.

In Globba, many such axillary buds at the base of the inflorescence axes do not produce flowers. The buds gradually become swollen into ovoid or globular structures (fig. 34.E,F), as the plant matures and flowers are produced towards the middle of the inflorescence axes. These ovoid or globular structures contain an accumulation of food substances for the developing bulbils. At about the middle of the season, when flowers are still opening on the plant, the axillary buds start to develop. The apical part grows faster than the root system and within a few weeks, new vegetative shoots are produced on the inflorescence axes (fig. 34.E,F; Plate 10.c). The food reserve is depleted and the small adventitious roots are produced. There may be up to 10 and 15 of such viviparous bulbils produced on a single inflorescence.

The weights may bend the frond down or the slightest disturbance could shake them off the parent plant. Such bulbils have been observed germinating into mature plants around the parent plant of Globba bulbifera grown in the greenhouse conditions. There is no doubt that such vegetative bulbils could develop rapidly into mature plants under natural environments.

The anatomy reveals that the axillary buds developed in the same way as all buds do, to produce new viviparous vegetative bulbils. The growing apex of the bud was protected by many overlapping sheaths which continue downwards to the node. In both transverse and longitudinal sections, many oblique and branching vascular elements were observed growing into the young bud from the fibrous cylinder of the inflorescence axis (fig. 36.B-E). The transverse sections taken further up on the bulbil show that these vascular elements are gradually arranged in the centre (fig. 36.E-G) of the new rhizome produced. A layer of thin-walled, narrow cells represents the endodermis and this separates the central cylinder from the cortex. The xylem elements are easily recognisable at this stage but the phloem cells are represented by small, narrow cells. Periderm is produced to the outer layers of the cortex (fig. 36.H). This consists of many layers of rectangular cells which have been produced by the rapid divisions of the parenchyma cells.

Away from the swollen rhizome base, the anatomy of the young vegetative shoot is similar to those of the mature shoot of the plant.

Apart from Globba, for which vegetative bulbils have been reported in the wild (Schumann 1904, Holttum 1950), these vegetative bulbils have not been reported in the wild for Hedychium greenii, Zingiber puberulum and Z. incomptum. These three plants were grown in the green houses under such conditions of high humidity and constant temperature. It is not known for

certain if some species of Globba set seeds, but in the majority of those seen in the herbarium, most produce bulbils. The bulbils probably have high survival value for the rapid establishment on the moist floor of the rain forest.

FIG. 34. VEGETATIVE BULBILS

Explanation in the text.

- A. Amomum cardamomum.
B, C. Hedychium greenii.
D. Zingiber puberulum.
E, F. Globba aurantiaca.

ax.b = axillary bud; bu = bulbil.

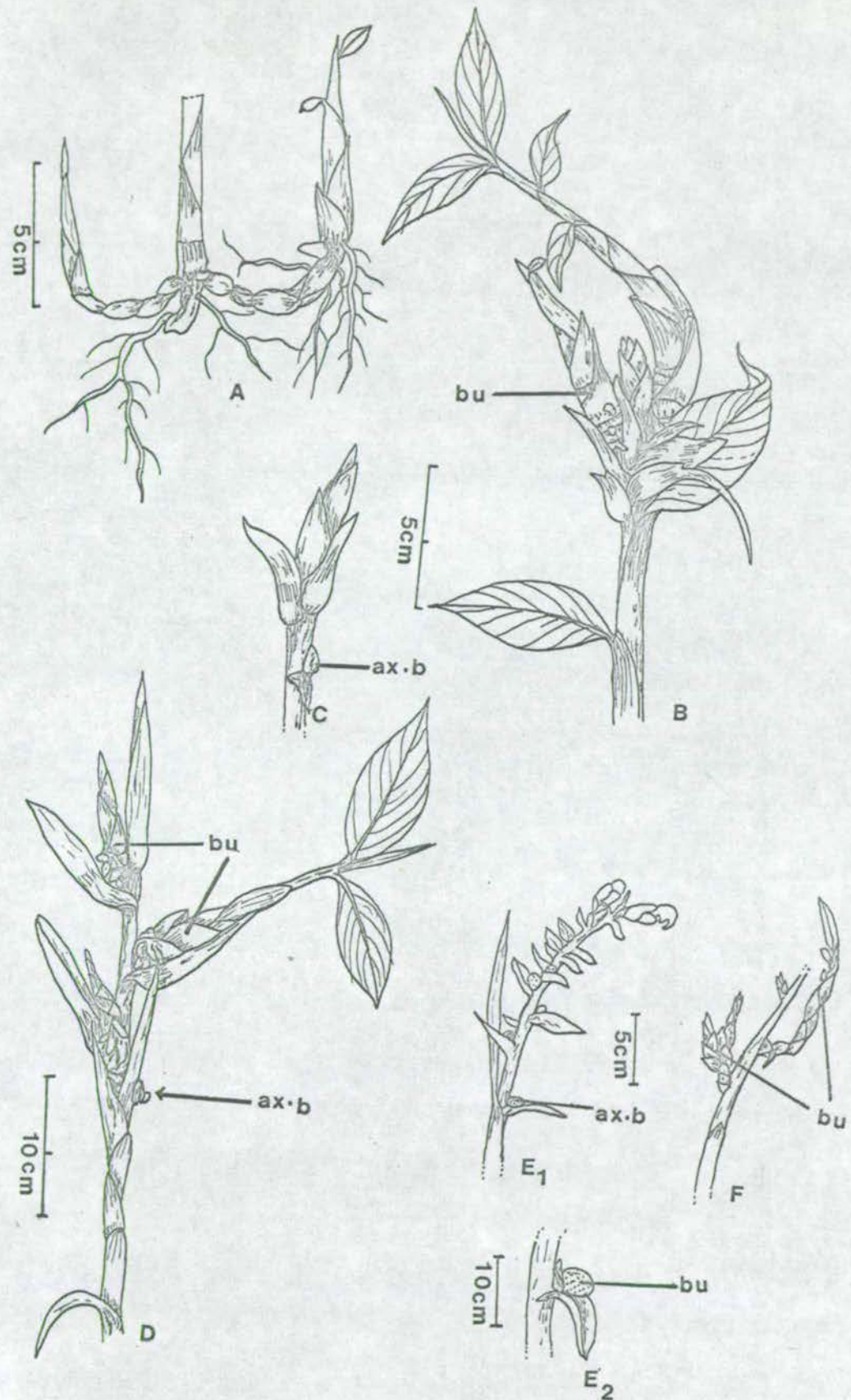
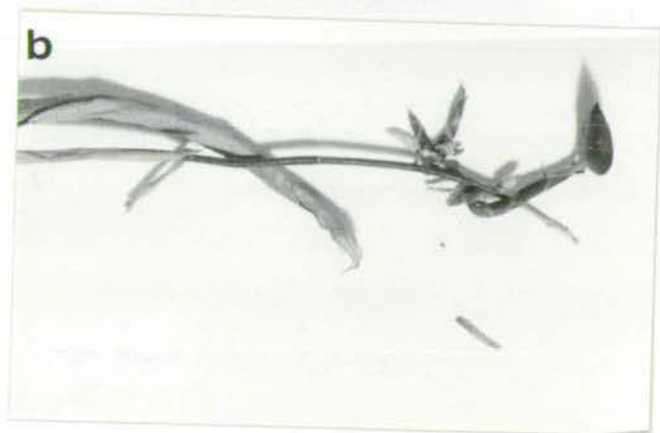


FIG.34

PLATE 10. VEGETATIVE BULBIL.

Explanation in the text.

- a. Hedychium greenii (x $\frac{1}{2}$)
- b. Globba aurentiaca (x $\frac{1}{3}$)
- c. Zingiber puberulum (x $\frac{1}{4}$)



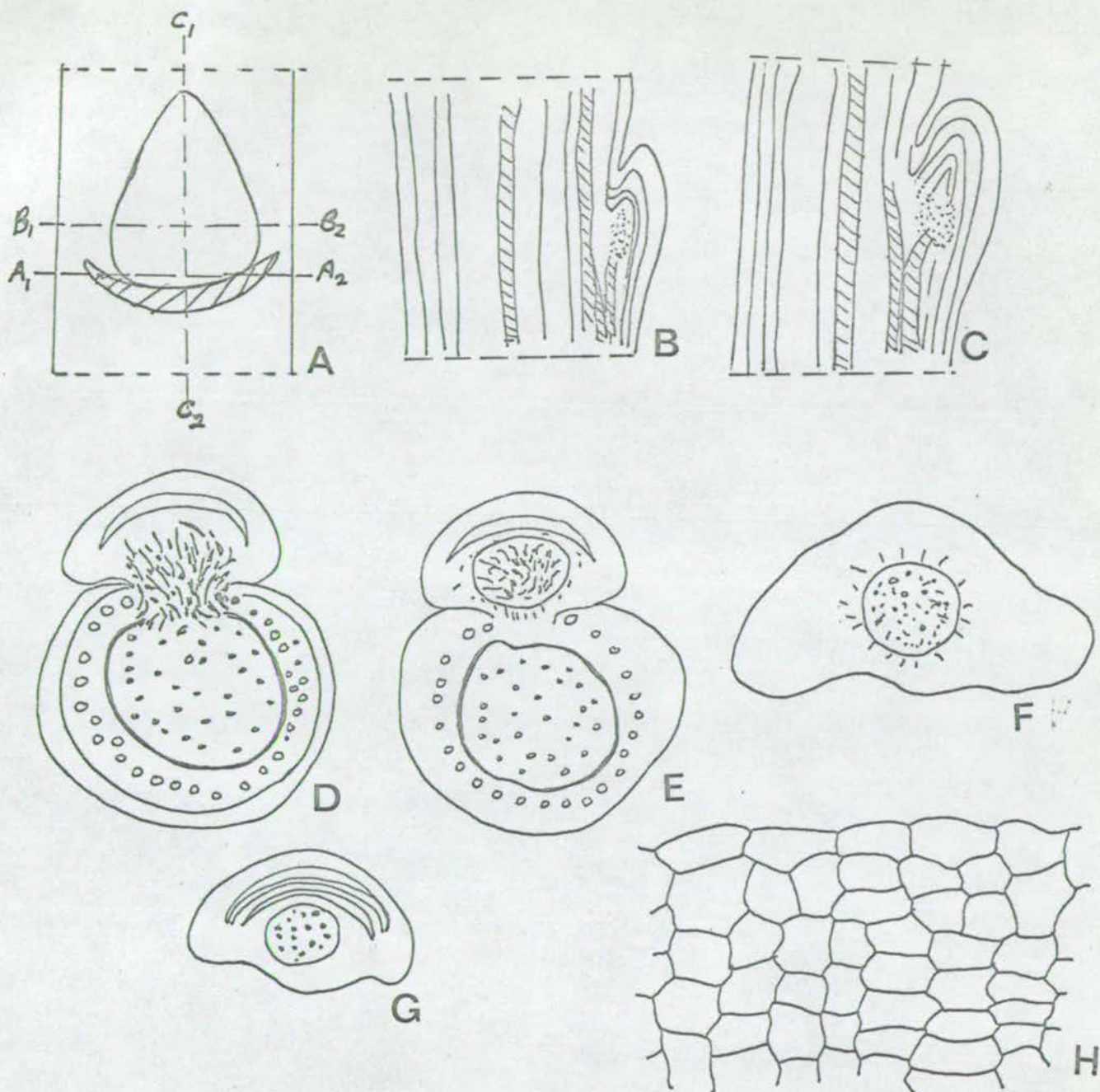


Fig. 35

FIG. 35. TRANSVERSE AND LONGITUDINAL SECTIONS
THROUGH A DEVELOPING BULBIL.

Explanation in the text

(A - H). Hedychium greenii.

Figures A x 5; B - C x 25; D - G x 7.5;
H x 180.

APPENDIX C.

DISTINCTIVE EPIDERMAL PATCH ON MIDRIB

In some species scattered through the family, a certain small area on the adaxial surface of the lamina midrib was observed to be differently coloured from the surrounding epidermal surface. This tissue patch is found on the lower half of the midrib (fig. 36 A), sometimes close to the base of the leaf in both old and young developing leaves. The shape varies from oval to elliptic and the size also varies between 4 - 6 x 2 - 3 mm. This tissue patch occurs singly except in Alpinia sp. (LAENG 1772) where there were two patches close together on the midrib.

This epidermal tissue was first observed on the cultivated specimens listed below and later it was detected on some of the herbarium material. The following are the few species on which this tissue has been observed:-

1. Burbidgea pubescens (fig. 36 A,B; 37 A,E-F).
2. B. stenantha.
3. B. sp. (B & M 5314, aff B. pubescens).
4. Amomum hewithii (fig. 37 B).
5. Globba atrosanguinea (fig. 37 C).
6. G. heterobractea.
7. Riedelia sp. - Cultivated N.G.F. 12400 (fig. 37 D).
8. Achasma megalocheilos.
9. Alpinia sp. (LAENG 1772).
10. Aframomum sp. (B. 4634).

The anatomy of this tissue was also investigated. In surface view epidermal strip of the patch shows that the cells in this area are smaller and much more thick-walled than the surrounding epidermal cells (fig. 36 B). The thickenings in the cell walls are similar to those of sclerenchymatous cells but they are unligified. The transition cells between the cells of this

tissue and normal epidermal cells are thickened on one side and at corners in a manner resembling the collenchymatous cells (fig. 36 B). Oil and/or tannin cells were present in the epidermal or sub-epidermal cells of this tissue, whereas they are absent from any other part on the adaxial surface of the midrib.

The transverse and longitudinal sections through this tissue (fig. 37 A-F), show that the epidermal cells are narrow and elongated radially. The height of these cells varies at the centre between two to four times the width. They become gradually reduced in height from the centre of the midrib to the edge of the tissue where the normal epidermal cells are found.

The outer walls of the cells are thickened and covered by a thick cuticle which is thicker in this zone than anywhere else on the midrib (fig. 37 E-F). The radial walls are also thickened. Some of the elongated epidermal cells contain oily substances which stained deeply in Sudan IV and some of these cells and/or tanniniferous substances were also observed in the sub-epidermal layers (fig. 37 E,F).

The formation of this tissue patch appears to be restricted to the epidermal cells within the small area where the difference in the colour of the midrib was observed. The other epidermal cells below and above it and those in the sub-epidermal layers appear to be less affected.

The function of this tissue is not known. However, it is probably of wide distribution in the family, especially in the tribes Globbeae and Alpinieae.

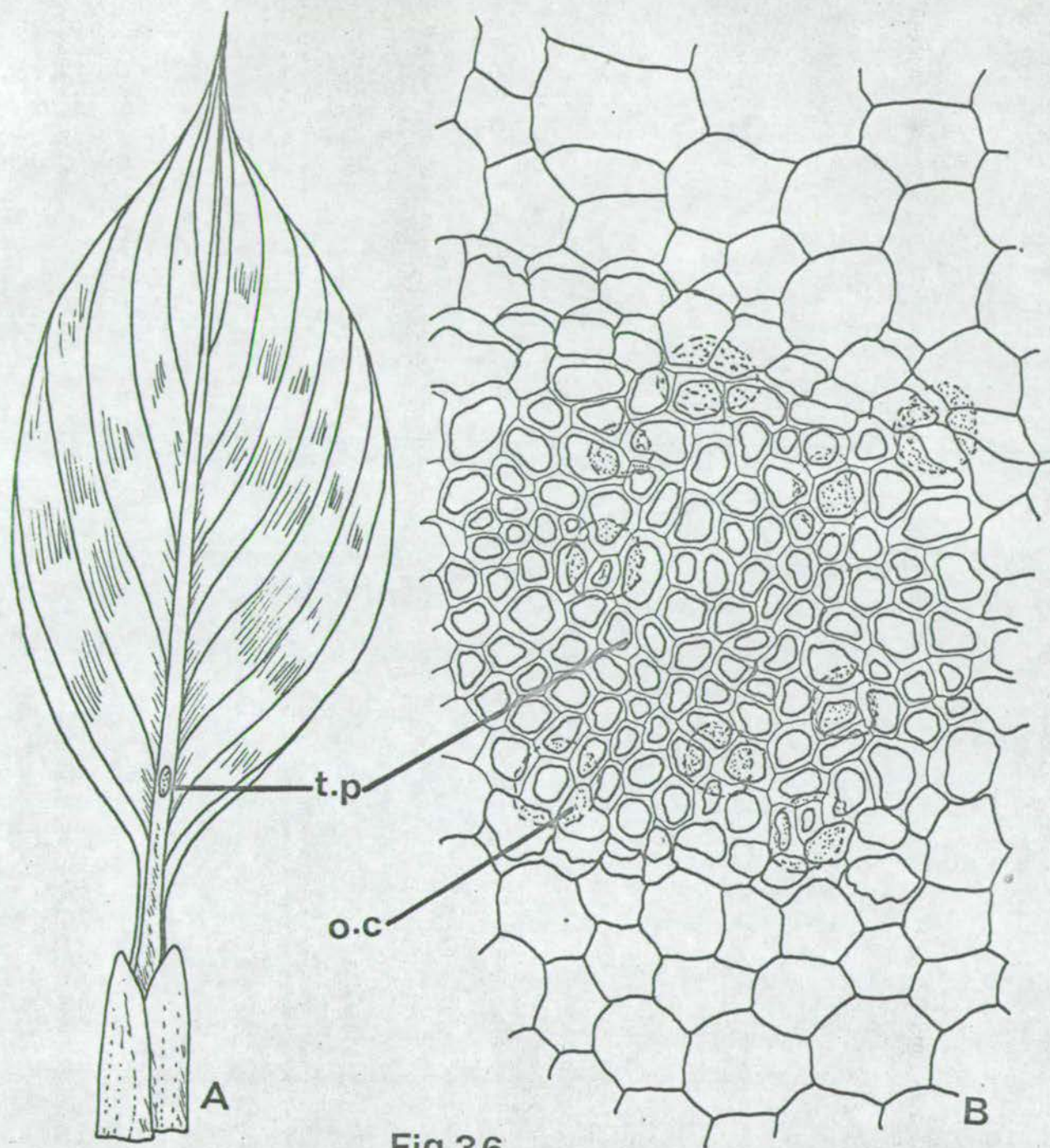


Fig.36

FIG. 36. EPIDERMAL TISSUE PATCH

A-B. Burbidgea pubescens. A. adaxial surface of lamina showing the midrib patch (t.p) (x 1). B. epidermal cells over the tissue patch. (x180)

o.c. = oil cell; t.p.= tissue patch.

FIG. 37. TRANSVERSE AND LONGITUDINAL SECTIONS
THROUGH PART OF THE TISSUE PATCH

Explanation in the text.

A. Burbridgea pubescens.

B. Amomum hewithii.

C. Globba atrosanguinea.

D. Riedelia sp. (N.G.F. 12400).

E. & F. Burbridgea pubescens.

e.c. = elongated cell; o.c. = oil cell;
t.p. = tissue patch.

Figures A - D x 31;

E - F x 680.

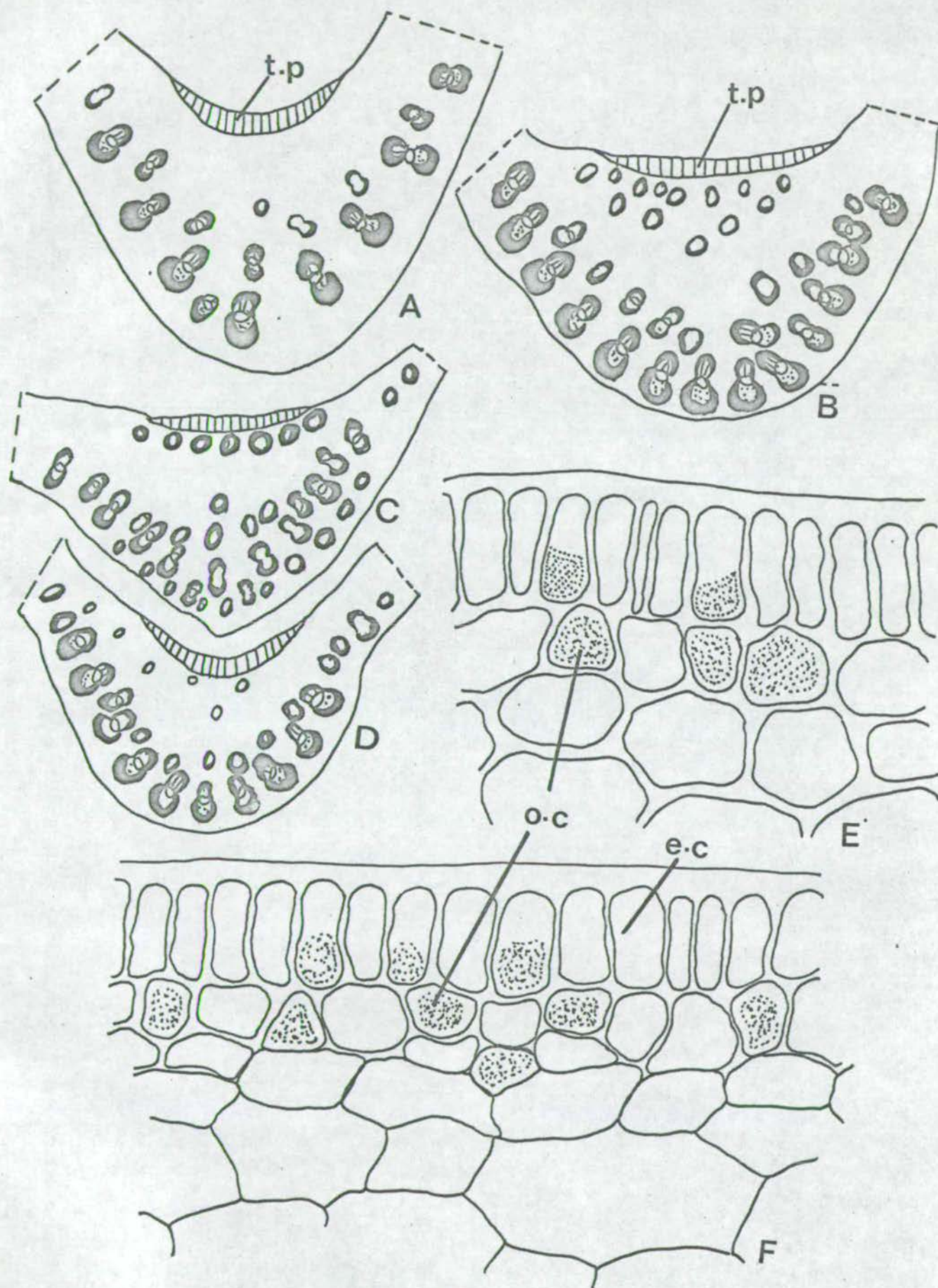


Fig.37

APPENDIX D.

LIST OF SPECIES EXAMINED

All the specimens are housed in the Herbarium and Gardens at Edinburgh. Species studied for stomatal development are marked (S).

SPECIES	COLLECTOR AND NUMBER
<u>ACHASMA</u> Griff.	
1. <u>brevilabrum</u> Val.	Burt 4983.
2. <u>macrocheilos</u> Griff.	
3. <u>megalocheilos</u> Griff.	(S) J. Sinclair 40244.
4. <u>subterraneum</u> Holttum.	Holttum 31212.
5. sp.	Burt 2477.
6. sp.	Burt 5279.
7. sp.	Burt 4753.
8. sp.	Burt 4721.
<u>ADELMERIA</u>	
9. <u>bifida</u> Ridl.	9637.
<u>AFRAMOMUM</u> K. Schum.	
10. <u>angustifolium</u> (Sonn) K. Schum.	Hilliard & Burt 4482.
11. <u>Daniellii</u> (Hook. f) K. Schum.	H.H. Johnston 13/5/1889.
12. <u>granum-paradisi</u> K. Schum.	J.M. Dalziel 1280.
13. <u>humburgii</u> K. Schum.	G. Zenker 2465.
14. <u>luteo-album</u> K. Schum.	(S) Hilliard & Burt 4634.
15. <u>melegueta</u> K. Schum.	(S) Cultivated C.
<u>ALPINIA</u> L.	
16. <u>allughas</u> (Retz) Rosc.	Wight 1053.
17. <u>blepharocalyx</u> K. Schum.	Forrest 12043.
18. <u>bracteata</u> Roxb.	J.H. Lace 5728.
19. <u>brevilabris</u> Presl.	A.D.E. Elmer 9531, 6853.
20. <u>calcarata</u> Rosc.	Dr. Hamilton 9.
21. <u>chinensis</u> Rosc.	J.L. Gressitt 1391.
22. <u>conchigera</u> Griff.	J. Sinclair 39264, 40550.
23. <u>elegans</u> (Presl) K. Schum.	A.D.E. Elmer 7866, 7258.
24. <u>formosana</u> K. Schum.	E.D. Merrill 1822.
25. <u>galanga</u> (= <u>langnas galanga</u> (L) Stuntz).	Griffith 5699.
26. <u>glabra</u> Ridl.	Burt 5221.
27. <u>graminacea</u> .	J. Sinclair 9538.
28. <u>haenki</u> (Presl) Merr. (<u>langnas haenki</u>).	A.D.E. Elmer 13866.
29. <u>intermedia</u> Gagnep.	S. Kitamura & G. Murata 2593.
30. <u>japonica</u> Miq.	S. Kitamura & G. Murata 639.
31. <u>latilabre</u> (= <u>Catimbium latilabre</u> (Ridl) Holttum.	J. Sinclair 40933.
32. <u>malaccensis</u> (Burm) Rosc.	(S) Cultivated.

33. *mutica* Roxb. (S)
34. *novae-pommeracea* (= *Catimbium novae pommeracea*) (K. Schum.) Holttum.
35. *officinatum* Hance.
36. *pahangensis* Ridley.
37. *parviflora* (Presl) Rolfe.
38. *penduliflora*.
39. *publiflora* Presl.
40. *pulchra* (Warb.) K. Schum.
41. *rufa* (Presl). K. Schum.
42. *samoensis* Reinecke.
43. *sandarae* Hort.
44. *speciosa* (Wendl.) K. Schum. (S)
45. sp.
46. sp.
47. sp. (aff. *A. rufa*).
48. sp. (aff. *A. flexistamen*).
49. sp. (aff. *versicolor*).
50. sp.
51. sp.
52. sp.
53. sp.
54. sp.
55. *subverticillata* Val.

AMOMUM L.

56. *biflorum* Jack.
57. *cardamomum* L. (S).
58. *dealbatum* Roxb.
59. *dictyocoleum* K. Schum.
60. *fusiforme* Ridl.
61. *hewithii* Ridl. (S).
62. *lepicarpa* Ridl.
63. *ovoideum* Pierre ex Gagnep.
64. *repoense* Pierre ex Gagnep.
65. sp.
66. sp.
67. sp.
68. sp.
69. sp.
70. sp.
71. sp.
72. sp. (*Geanthus* sp.)
73. sp.
74. sp.
75. sp.
76. *trilobium* Ridl.
77. *xanthophebum* Bak.

BOESENBERGIA Kuntze.

78. *grandifolium* (Wall) Merril
79. *hutchinsonii* Burt & Smith.
80. *longiflora* Wall.

Cultivated. 210:34.

- J.C. Whitmore 6018.
 O.F. Baker 114.
 J. Sinclair 40147.
 Cuming 1327.
 J. Sinclair 7288.
 O.M. Ramos & F.W. Foxworthy 13195.
 T.C. Whitmore 6024.
 C.A. Wenzel 284. M. Ramos 10934.
 H.S. McKee 2787.
 Cultivated.
 Cultivated 4959.
 A.D.E. Elmer 7287.
 W.T. Tsang 27121, 29108.
 A.D.E. Elmer 14051, 9078, 9578.
 Burt 5300.
 Burt 5166.
 Burt 5289.
 J. Score 2316.
 Corner 106, 107.
 Burt 4876.
 Burt 5221.
 T.C. Whitmore 2056.

- L. Pierre 554.
 Cultivated.
 C.H. Cave 19/5/1913.
 Burt 4722.
 A.D.E. Elmer 9509.
 Cultivated B 2478.
 A.D.E. Elmer 10384.
 L. Pierre 542.
 L. Pierre 625.
 Burt 4811.
 Burt 5342.
 Burt 5337.
 Burt 5303.
 Burt 5341.
 Burt. 5366.
 Burt 5020.
 Burt 5343.
 S.K. Lau 408.
 A.N.G. Alston 14115.
 Burt 5272.
 A.D.E. Elmer 9077.
 Burt 5159.

- Burt 2430.
 Burt 2235.
 J.H. Loe 5403.

81. *parvula* J. Keenan, U Tun Aung & R.H. Rule 1399.
 82. *plicata* L. Moysey & Kiah 33864.
 83. *sp.* (S) B. & M. 5164.
 84. *sp.* (S) Burt 5146.
 85. *sp.* Burt 4900.
 86. *sp.* (S) Burt 5548.
 87. *sp.* (S) Burt 4927.
 88. *sp.* Burt & Woods 2700.
 89. *sp.* (S) Burt 4706.
 90. *sp.* Burt 2273.
 91. *sp.* Burt 2064.
 92. *sp.* Burt 2308.
 93. *sp.* Burt 2107.
 94. *sp.* Burt 2489.
 95. *sp.* Burt 2072.
 96. *sp.* Coode 69.0865.
- BRACHYCHILUM O.G. Peters.
 97. *horsfieldii* O.G. Peters. (S) Cultivated U6.1677.
- BURBIDGEA Hook. f.
 98. *pubescens* (S) B. & M. 4822.
 99. *stenantha* B. & M. 4821.
 100. *sp.* B. & M. 5314.
- CAMPTANDRA Ridl.
 101. *angustifolia* Ridl. Burt & Woods 2507.
 102. *fongyuensis* Gagnep. G. Forrest 12983.
 103. *latifolia* Ridl. (S) Woods 996.
 104. *parvula* (King) Ridl. (S) J. Sinclair & Kiah 38699.
 105. *yunnanensis* (Gagnep) K. Schum. Dr. Heiner Handel. Mazzettii 7254.
- CAULOCAEMPFERIA Larsen.
 106. *coenobialis* (Hance.) Larsen. W.T. Tsang 20595.
 107. *linearis* (Wall) Larsen. Wall Cat. 6592.
 108. *secunda* (Wall) Larsen. E.J.C. Hook.f. & Thomson.
 109. *sikkimensis* (King) Larsen. R.E. Cooper 1038.
- CAUTLEYA Royle.
 110. *gracilis* Smith. G. Forrest 15495, 21951, Kingdom Ward 3200.
 111. *lutea* Royle. G. Forrest 7009, 4805, 8435.
 112. *robusta* Bak. (S) Cultivated NH.59.760.
 113. *spicata* (Smith) Bak. Stainton, Sykes & Williams 6503.
 114. *sp.* (aff. *lutea*). F. Ludlow, G. Sherriff & J.H. Hicks 20836.
- CENOLOPHON Holttum.
 115. *Cornerii* Holttum. E.J.H. Corner 30506.
 116. *oxymitrum* (K. Schum). Holttum. W.G. Craib 2069.
 117. *sp.* Burt 4989.
 118. *sp.* J. Sinclair 39264, 40550.
 119. *sp.* Burt 2268.

- CLENKOWSKYA Solms.
 120. *aethiopica* Solms - Leub.
 121. *aethiopica* Solms - Leub. var. *angustifolia* Ridl.
 122. *pleiantha* K. Schum.
 123. *rhodesica*.
 124. *rosea* Schweinf.
 125. *zambesiaca*.
 126. sp. (Nyasaland).
CURCUMA L.
 127. *gracillinia* Gagnep.
 128. *longa* L. (S)
 129. *xanthorrhiza* Roxb.
 130. sp. aff. *sessilis*.
 131. sp.
 132. sp.
CYPHOSTIGMA Benth.
 133. *pedicellatum* K. Schum.
ELETTARIA Maton.
 134. *cardamum* Maton.
 135. *surculosa* K. Schum.
 136. *stoloniflora* K. Schum.
 137. sp.
 138. sp.
 139. sp.
GEOCHARIS (K. Schum.) Ridley.
 140. sp.
GEOSTACHYS Ridl.
 141. *taipengensis* Holttum.
 142. sp. aff. *penengensis*.
GLOBBA L.
 143. *atrosanguinea* Teijsm & Binn. (S)
 144. *aurantiaca* Miq. (S)
 145. *bulbifera* Roxb. (S)
 146. *bulbosa* Gagnep.
 147. *campeophylla* K. Schum.
 148. *clarkei* Bak.
 149. *curtissii* Holttum.
 150. *garrettii* Kerr.
 151. *heterobracteata* K. Schum.
 152. sp. aff. *Hookerii*.
 153. *Kerrii* Craib.
 154. *leucantha* Miquel.
 155. *orixensis* Roxb.
 156. *pendula* Roxb.
 157. *racemosa* Smith.
- G. Adamson 322.
 H. Baum 518.
 H. Baum 168.
 R.B. Drumond & A.J. Cookson, 6759, 6200.
 B.L. Burt & O.M. Hilliard 4102.
 J. Buchanan 191.
 L. Pierre.
 Cultivated. Woods 115.
 J. Sinclair 40295.
 A.F.G. Kerr 634.
 A. Campbell 8114.
 G. Forrest 8322.
 Grieson 1049.
 C.F. Baker 128.
 Burt 2504.
 Burt 4773.
 Burt 2577.
 Burt 2085.
 Burt 5144.
 Burt 2869.
 J. Sinclair 38694.
 Burt 2827.
 Cultivated 4079.
 Cultivated.
 Cultivated.
 J. Linsley Gressitt 1374.
 A.D.E. Elmer 7278.
 J.D.A. Stainton 768.
 E.J.H. Corner 33193.
 H.B.G. Garrett 753.
 Cultivated 4082.
 C.H. Cave 15/7/13.
 A.F.G. Kerr 1278.
 J. Sinclair 20/2/51.
 S.S. Chiem 5998.
 J. Sinclair 38681.
 E.J.H. Corner 6535.

158. *schomburgkii* Hook. f. Cultivated 5422.
 159. *tricolor* Ridley. Burt & Woods 2825.
 160. *unifolia* Ridley var. *sessiliflora* Holttum. E.J.H. Corner 30013.
 161. *winitii* Wight. (S) Cultivated 4085.
 162. *yeatsiana* Craib. A.F.G. Kerr 1214.
 163. sp. aff. *leucantha*. Burt 5175.
 164. sp. Burt 5523.
 165. sp. Steward et al 570.
 166. sp. C.H. Cave 6/7/15.
- HAPLOCHOREMA K. Schum.
 167. *uniflorum* K. Schum. (S) Cultivated B 4775.
 168. *oligospermum* K. Schum. Burt 2885.
- HEDYCHUM Koenig.
 169. *aurantiacum* Wall. Stainton, Sykes & Williams 6439.
 170. *coccineum* Buchan-Ham. Cultivated 4352.
 171. *coccineum* var. *angustifolium*. Cultivated 4485.
 172. *coccineum* var. *longifolium*. Rose. J.H. Lacey 5303.
 173. *coronarum* Koenig. (S) Cultivated.
 174. *cylindricum*. Cultivated. B. & M. 5382.
 175. *densiflorum* Wall. (S) Cultivated 4122, 5218.
 176. *elatum* R. Br. R.E. Cooper 1165.
 177. *ellipticum* Ham ex Smith. W.G. Craib 788, 1304.
 178. *flavescens* Carey. Cultivated 3924.
 179. *forrestii* Diels. (S) Cultivated 82;57.
 180. *gardnerianum* Rose. (S) Cultivated 406;26.
 181. *gracile* Roxb. var. *glaucum* Rose. Cultivated.
 182. *greenii* W.W. Smith. (S) Cultivated 4373.
 183. x *Raffillii*. Cultivated 4480.
 184. *spicatum* Buch - Ham. G. Forrest 28920.
 185. *thyrsiforme* Ham. ex Smith. Cultivated 449.
 186. *venustum* Wight Cultivated GL 61:1273.
 187. *villosum* Wall. Col. Johnstone 1930/31.
 188. *yunnanense* Gagnep. A.K. Bulley 4811.
- HITCHENIA Wall.
 189. *careyana* Wall. Wall Cat. 6595.
 190. *glaucum* Wall.
- HORNSTEDTIA Retz.
 191. *conoides* Ridl. A.D.E. Elmer 10246.
 192. *leonurus* (Koeng.) Retz. J. Sinclair 9/7/49.
 193. *lophophora* Ridl. A.D.E. Elmer 10365.
 194. *microcheila* Ridl. A.D.E. Elmer 10279.
 195. *philippinensis* Ridl. A.D.E. Elmer 10270.
 196. *pininga* Val. Burt 5152.
 197. *scyphifera* (Koeng) Retz. J. Sinclair 6/1/49.
 198. *scyphifera* var. *fusiformis* Holttum. E.J.H. Corner 30236.
 199. *villosa* Valet. Burt 4790.

200. sp. Woods 1738.
 201. sp. Burt 5402.
 202. sp. Burt 2824.
 203. sp. Burt 5158.
 204. sp. Burt 5306.
 205. sp. Burt 5057.
- KAEMPFERIA L.
 206. *angustifolia* Rosc. Cultivated 4078.
 207. *elegans* Wall. (S) Cultivated 3926.
 208. *gilbertii* Bull. Cultivated 673031.
 209. *marginata* Carey. J.W. Helfer 119.
 210. *pandurata* Roxb. Mangalor, Ostindien.
 211. *pulchra* Ridl. (S) Cultivated 4341.
 212. *rotunda* L. (S) Cultivated 4219.
 213. sp. J. Keenan et al 1302.
 214. sp. J. Keenan et al 1221.
 215. sp. J. Keenan et al 1342.
- MANTISIA Sims.
 216. *spathulata* Schult. W.J.L. Wenger 331, 332.
 217. *wardii* Burt & Smith. (S) F. Kingdom Ward 22356.
- PHAEOMERIA Lindl.
 218. *magnifica* R. Schum. (S) Cultivated.
 219. *speciosa* (Bl) Merr. Burt 5141; J. Sinclair 40891.
 220. *venusta* (Ridley) K. Schum. J. Sinclair 10596.
- PLAGIOSTACHYS Ridl.
 221. *albiflora* Ridley. T. Sinclair 39674.
 222. *pardosa* Ridl. A.D.E. Elmer 8568.
 223. sp. aff. *borneensis*. Burt 2703.
 224. sp. Burt 4793.
 225. sp. Burt 5161.
 226. sp. Burt 4718.
 227. sp. Burt 5505.
 228. sp. Burt 5421.
 229. sp. Burt 2808.
 230. sp. Burt 2818.
 231. sp. Burt 5429.
- RENEALMIA L.
 232. *antillarum* Gagnep. P. Sintenis 1578.
 233. *bracteosa* Griseb. W.E. Broadway 4/8/13.
 234. *cabraei* De Wild, et Dur. G. Zenker 1166.
 235. *cincinata* Bak. D.W. Afriva 1348.
 236. *dermatopetala* K. Schum. N.L. Britton & H.H. Rusby 2566.
 237. *exaltata* (L) Rosc. P. Sintenis 2608.
 238. *fischeri* K. Schum. - 525.
 239. *micrantha* K. Schum. N.L. Britton & H.H. Rusby 2566.
 240. *occidentalis* Swartz. Chas. C. Deam 6035.
 241. *polyantha* K. Schum. G. Zenker 2546.
 242. *racemosa* (L) A. Rich.

243. *sessiliflora* Gagnep. W. Jameson 558.
 244. *spicata* Gagnep. Jose Stemibain 7442.
 245. *sp.* G. Zenker 3493.
 246. *sp.* H.H. Smith 2657.
- RHYNCHANTHUS Hook.
 247. *beesanus* W.W. Smith. G. Forrest 8108, 18439, 15830;
 F. Kingdom Ward 3485.
 248. *longiflorus* Hook. f. Capt. R.W. McGregor 832.
 249. *sp.* J. Keenan et al 3107.
 250. *sp.* J. Keenan et al 3250.
- RIEDELIA Oliv.
 251. *sp.* A.N. Millar 14594.
 252. *sp.* P.F. Hunt 2358.
 253. *sp.* N.G.F. 12400.
- ROSCOEIA Smith.
 254. *alpina* Royle. Cultivated 289.
 255. *auriculata* K. Schum. Cultivated 3505.
 256. *capitata* var. *purpurata*. G. Forrest 4809.
 257. *cautleoides* Gagnep. (S) Cultivated; F.K. Ward 5269.
 258. *chaemaeleon* Gagnep. G. Forrest 21527.
 259. *humeana* Balf. et Sm. Cultivated.
 260. *intermedia* Gagnep. G. Forrest 19236.
 261. *purpurea* Smith. (S) Cultivated.
 262. *procera* Auderron 44.
 263. *yunnanensis* var. *scillifolia*. G. Forrest 21527.
- SCAPHOCHLAMYS Holttum.
 264. *atroviridis* Holttum. E.J.H. Corner 30240.
 265. *breviscarpa* Holttum. E.J.H. Corner 30021.
 266. *erecta* Holttum. E.J.H. Corner 31941.
 267. *grandis* Holttum. E.J.H. Corner 30030.
 268. *klossii* (Bak) Holttum. E.J.H. Corner 30951.
 269. *kunstleri* (Bak) Holttum. (S) E.J.H. Corner 31674.
 270. *perakensis* Holttum. E.J.H. Corner 31690.
 271. *rubromaculata* Holttum. E.J.H. Corner 30031.
 272. *tenuis* Holttum. E.J.H. Corner 30543.
- Woods specimens (New Guinea) aff. Boesenbergia.
 273. *Woods* 1562.
 274. *Woods* 1732.
 275. *Woods* 1549. (S)
 276. *Woods* 1574.
 277. *Black* 67.1337.
- ZINGIBER Adans.
 278. *bradleyanum* Craib. A.F.C. Kerr 763.
 279. *capitatum* Roxb. Col. Gentins
 280. *cassumunar* Roxb. J.H. Lace 5407.
 281. *clarkei* King. Major D. Prani.
 282. *cylindricum* Moon. Meebold 9085.
 283. *gracilis* var. *petiolata* Holttum. E.J.H. Corner 31570.

284. *griffithii* Bak.
 285. *incomptum* Burt & Smith.
 286. *inflexum* Blume.
 287. *kerrii* Craib.
 288. *kunstleri* King.
 289. *mioga* (Thumb) Rosc.
 290. *mollis* Ridl.
 291. *multibracteata* Holtum.
 292. *odoriferum* Blume.
 293. *officinale* Rosc.
 294. *puberulum* Ridley.
 295. *roseum* Rosc.
 296. *smilesianum* Craib.
 297. *striolatum* Diels.
 298. *zerumbet* (L) Smith.
 299. *sp. aff. rubens.*
 300. *sp. (epiphytic).*
 301. *sp.*
 302. *sp. aff. coloratum.*
 303. *sp.*
 304. *sp.*
 305. *sp.*

(S)
(S)

(S)

Burt 2831.
 Cultivated 08.0851.
 A.F.G. Kerr 1290.
 J. Sinclair & Kiah 38784.
 Yokohama Nursery 1908.
 A.D.E. Elmer 9843.
 E.J.H. Corner 33174.
 Burt 5302.
 Cultivated 4914.
 J. Sinclair 10622.
 J.H. Lacey Nov. 1902.
 W.G. Craib 1311a.
 H.F.H. Mazzetti 12988.
 Cultivated 69:0904.
 J.H. Lacey 5425.
 Burt 4875.
 Woods 597.
 B. & M. 5127.
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 K. Jana.

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ABSTRACT OF THESIS

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Degree DOCTOR OF PHILOSOPHY Date SEPTEMBER 1970
Title of Thesis "TAXONOMIC STUDIES IN THE ZINGIBERACEAE WITH SPECIAL REFERENCE
TO VEGETATIVE CHARACTERS"

Vegetative material for about three hundred and five species belonging to about thirty-three genera in the Zingiberaceae were examined.

The occurrence, variation and different patterns of distributions of about eighty-six vegetative and anatomical characters are described and tabulated.

The contribution of the anatomical features to the taxonomy of the family is discussed. The family is characterised anatomically, but the separation of the tribes on the basis of anatomical features is weak. However, certain genera and species are characterised by their distinctive anatomical features. The following particular suggestions are presented:

- (i) That the African species of Kaempferia should be separated from the Asiatic species as the genus Cienkowskya. This suggestion is justified on both anatomical and cytological grounds.
- (ii) That the genus Zingiber be separated as a distinct tribe Zingibereae (sensu stricto). This genus has been taking an exceptional position in the past classifications. Its separation into a tribe of its own is supported by its unique anatomical characteristics.

Other contributions include the demonstrations of the anatomical distinction between the closely related genera Renealmia and Alpinia.

The stomatal development was studied in thirty-six species; it is always perigenous and the stomata are predominantly tetracytic. Polycytic stomata also occur but with less frequency, except in Boesenbergia and Camptandra where polycytic stomata are more frequent than the tetracytic type.

Certain evolutionary progressions within the family are suggested.

The genera are grouped together according to their anatomical similarities. Both an indented and a synoptic key is made for some of the genera.

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